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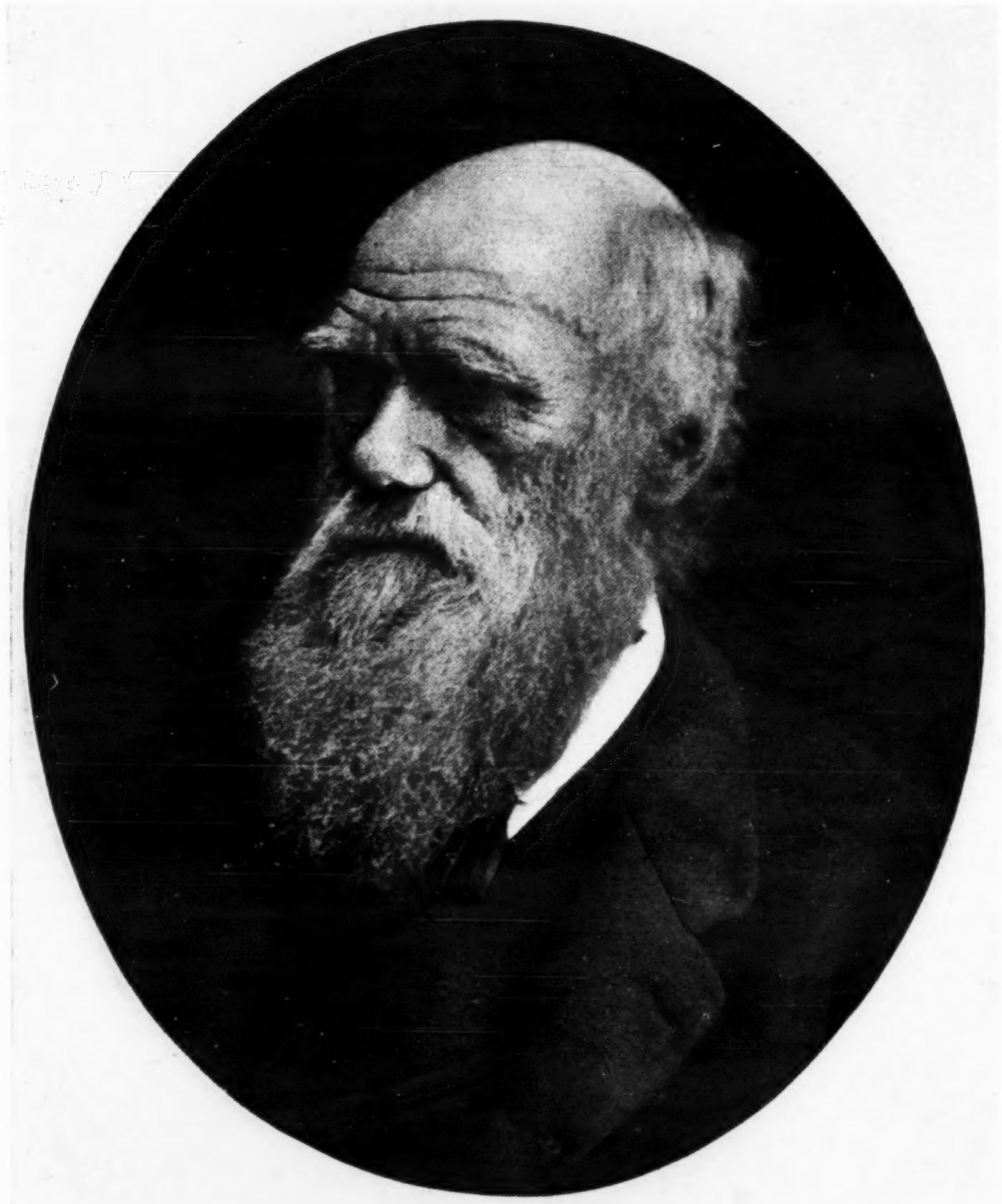

Ch. Darwin

"Some old members of the Royal are quite shocked by my having the Copley."

VOLUME 21 AUGUST, 1930 NUMBER 8

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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The

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Vol. XXI AUGUST, 1930 No. 8

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COMING

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Benjamin Franklin coined the phrase, and since his time the evidence confirming Franklin's view has been increasing. The process bears a curious resemblance to the economic phenomenon known as Gresham's Law.

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Estimates vary as to their number: if there are only a million the situation is serious enough; if there are six million it is perhaps more than six times as alarming in an increasingly complicated environment where those with an average mental equipment have their hands full keeping "ahead of the game."

Genetics of Plants and Animals

Brevis Maize—A Skull and Ear Defect in Swine—A Chromosomal Chimera in Tobacco—The Silver Mouse—Non-Heritable Downlessness in Fowls—A New Pod Color in Beans—Fertile Mules Again.

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THE HOME OF CHARLES DARWIN

Frontispiece

DARWIN moved to Down House in September, 1842, and wrote prophetically, "My life goes on like clockwork, and I am fixed in the spot where I shall end it." Afflicted as he was with chronic ill health such a mode of life was of paramount importance in enabling him to continue his chosen work for so many years, and only on rare occasions did he leave this house, with an environment "whose chief merit is its extreme rurality." A short time before he moved to Down he wrote that he had "allowed myself the satisfaction of writing a very brief abstract of my theory in pencil in 35 pages." Not until seventeen years later (November, 1859) was the *Origin of Species* published. Three years after Darwin's death (April 19, 1882) Huxley summed up his contribution in these words:

> The causes of this deep and wide outburst of emotion [occasioned by Darwin's death] are not far to seek. We had lost one of these rare ministers and interpreters of Nature whose names mark epochs in the advance of natural knowledge. For, whatever be the ultimate verdict of posterity upon this or that opinion which Mr. Darwin has propounded; whatever adumbrations or anticipations of his doctrines may be found in the writings of his predecessors; the broad fact remains that, since the publication and by reason of the publication, of the *Origin of Species* the fundamental conceptions and the aims of the students of living Nature have been completely changed.

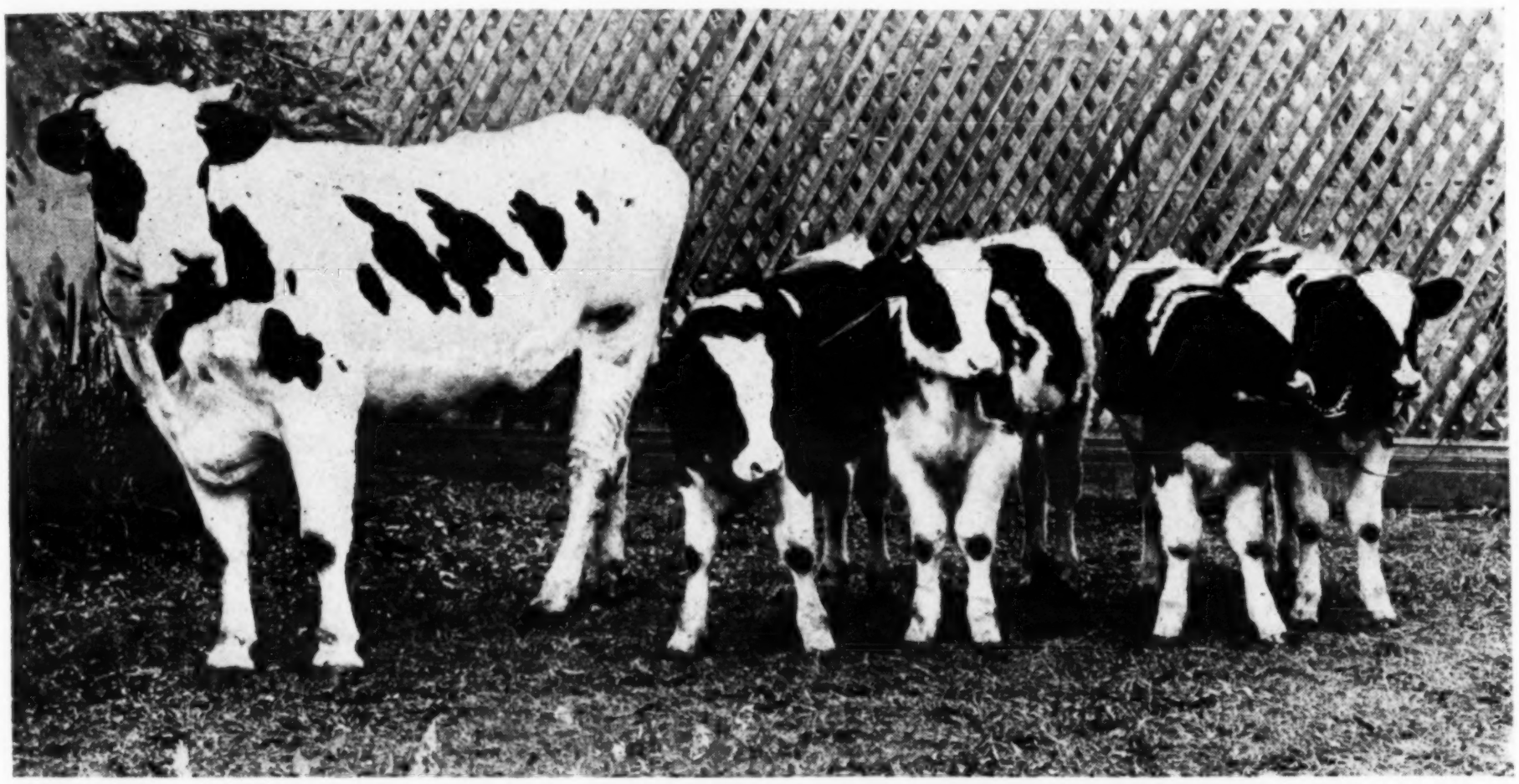
(The Copley Medal, mentioned on the cover, is the highest honor which the Royal Society can confer. It was awarded to Darwin in 1864.)

BOVINE QUADRUPLETS

Including Twins Apparently Monozygotic

F. B. HUTT

Division of Poultry Husbandry, University of Minnesota



AAGIE SEGIS CALAMITY AND HER FOUR CALVES

Figure 1

From left to right—dam, bull, free-martin, heifer, heifer, the latter two being the pair considered monozygotic. If the twins are actually identical two very unusual phenomena are thus represented, for quadruplet calves occur only with extreme rarity, (probably not more often than two sets in a million births), and identical twins in cattle are so uncommon that some biologists doubt their existence.

SOME time ago there came to the attention of the writer a case of multiple births in cattle which presents some features of particular interest to biologists. It has not been possible to secure as much information as could be desired about this case, but further study has been rendered impossible by the slaughtering of the animals concerned. The data available are therefore presented herewith.

On July 2, 1925, Aaggie Segis Calamity, a Holstein-Friesian cow belonging to Mr. W. E. Lawson, of Hayfield, Manitoba, Canada, and registered in the herd books of The Holstein-Friesian Association of Canada as No. 83496, gave birth to four living calves (Figure 1). These were sired by the bull, Hector Colanthus Fayne, No. 56351.

The dam was born on Sept. 24th, 1918, and was thus almost seven years old when her quadruplets were dropped. Prior to her greatest achievement this cow had had two bull calves at single births and had produced 19,215 lbs. of milk, with an average fat content of 3.47 per cent, in her second lactation period. At her fourth calving (*i. e.* the one following

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the birth of quadruplets) Aaggie Segis Calamity dropped twins, a bull and a heifer, the latter of which died soon after.

Quadruplets

Special interest is centred, not in the dam, but in the quadruplets. They have naturally received a considerable amount of newspaper publicity and have also been illustrated in several journals.[2, 3, 21]. They made an interesting side-show exhibit for an amusement company operating at the Manitoba Provincial Fair in July, 1926, and three of them were also entered for competition in the regular classes where two of them (heifers) were placed third and fourth and another (the bull) won fifth prize in their respective sections.

Births of three or more at a time are unusual in uniparous species, but, when they do occur, it is still more unusual for all of such offspring to be alive and healthy as were these four. De Bruin[5] reviews several cases of multiple bovine pregnancies reported in veterinary literature, including two cases of quadruplets, but does not state how many of these calves lived to maturity. In one instance, quintuplets lived to eight days. In another sextuplets were prematurely born following an injury. This author and Pearl[19] both quote from McGillivary's *Manual of Veterinary Science and Practice* (1857) the case of a cow which produced 25 calves in eight years, including two sets of quadruplets (not those referred to above) and one set of sextuplets. All of the latter died prematurely. Concerning one set of quadruplets no record of death or survival was given but in the other case three of the four calves lived. Other instances of bovine quadruplets are cited by Bissonnette.[4]

The number of possible ways in which quadruplets might arise is rather large to permit of any accurate calculation of the theoretical frequency with which such an event might be expected to occur. This is especially so in the case of the domestic ox, for in this species there has been some doubt whether monozygotic twinning ever occurs or not, so that the extent to which it might influence the frequency of quadruplets can not be computed.

Jones and Rouse[10] found in a study of Hereford and Aberdeen Angus herd books only one case of quadruplets among 747,100 births. This number of births is not enough to establish the frequency of bovine quadruplets, especially since these records do not include still-born calves, but the ratio is not out of line with those given for man, also an uniparous species, by various investigators, as recently summarized by Jenkins[9] and Greulich:[7]

	Number of births	*Quadruplets birth ratio*
Veit. Prussia, 1826-1849	13 million	1 : 371,694
Neefe, 1877	50 million	1 : 551,368
Prinzing, Germany, 1871-80	63 million	1 : 778,688
Arey		1 : 750,000
Guzzoni		1 : 757,000
Greulich	120 million	1 : 670,734

Monozygotic Twins

The writer is of the opinion that the case reported in this paper persents a phenomenon even rarer than the birth of quadruplets, inasmuch as there are good reasons for believing that this particular set resulted from coincident dizygotic and monozygotic twinning.

The quadruplets included one bull and three heifers. One of the latter was found upon examination by Dr. Harry Ross, of Brandon, the attendant veterinarian, to be a free-martin, and although attempts were subsequently made to get her bred, these were unsuccessful. When the four calves were seen by the writer in July, 1926, it was at once evident that the two other heifers, both apparently normal, presented every indication of being identical twins.

THE QUADRUPLETS AT 7½ MONTHS

Figure 2

From left to right—dam, bull, free-martin, heifer, heifer. Quadruplet calves rarely survive the first few days of life, and to have all of them reach maturity is most unusual.

Reversed Asymmetry

This was attested in part by the striking uniformity of size and conformation which they exhibited, but particularly by the distinct reversed asymmetry, or "mirror-imaging," displayed in their colour patterns.

This phenomenon is most apparent in conjoined monsters where it is frequently found as *situs inversus viscerum*, a condition wherein one individual (*i. e.* one half of the monster) has such unpaired organs as the heart, aortic arch and stomach in the normal position on one side of the body, while in the other half of the monster those same organs are found on the opposite side of the body. This condition is apparently no commoner in separate human twins than in persons born at single births, but Wilder[23] has shown that reversed asymmetry is sometimes found in the palm or finger patterns of monozygotic twins. In such cases the pattern of the left hand, or of the left index-finger of one twin, resembles the right hand or right index-finger pattern of the other and vice versa. Other examples of mirror-imaging in human twins, including non-genetic left handedness and counter-clockwise hair-whorl, are discussed by Verschuer[22] and Newman.[17, 18] The latter writer found reversed asymmetry of double bands and other characters so frequent in the armadillo, *Dasypus novemcinctus*, that he concluded that "the occurrence of symmetry reversal or mirror-imaging in twins or double monsters may safely be taken as a criterion of their monozygotic origin."

Presumably this condition arises from the early separation of primordia which were originally destined to give rise to the right and left sides of the body. Most vertebrates are in general bilaterally symmetrical but exhibit asymmetry in certain unpaired organs and in such small details as the variations in colour pattern, and (in man) right or left-handedness, or the direction of hair-whorl. When one zygote gives rise to two individuals, this asymmetry is not always retained in each animal and in some instances the phenomenon of reversed asymmetry is brought about. A con-

siderable body of evidence brought together by Newman[18] indicates that whether non-conjoined twins appear identical or exhibit asymmetry reversal depends, respectively, upon whether twinning takes place before the symmetry and asymmetry of the embryo are established or during that process.

The writer is not aware of any published account of mirror-imaging of any character in separate bovine twins. Such a condition is more likely to be noticed in those breeds in which white spotting is a characteristic than in self-coloured animals.

Kröning[11] in his study of the colour patterns of double monsters in cattle, swine, cats and goats, illustrates two cases of conjoined calves which exhibit marked reversed asymmetry. In one of these (Case 10.) the white blaze on one forehead lies much to one side and is of an unusual pattern. This is replicated almost identically on the other head but as a mirror image. Similarly his Case 23, in which the two calves are joined only at the thighs, illustrates the same phenomenon but with a considerable degree of variation in small details.

Williams[24] illustrates three specimens of conjoined monsters in the museum of the New York State Veterinary College concerning which he says: "As far as the fission extends, the markings are inversely identical. The proximal sides of the divided parts are marked inversely alike, and the distal sides follow the same rule. Had the fission been completed and the plan of marking persisted, the color markings, when the calves were standing side by side or head to tail would have been unlike, but when standing head to head or tail to tail, would have been inversely identical. That is, a photographic negative of either side of one calf, turned end for end, would be the negative of the opposite side of the other calf."

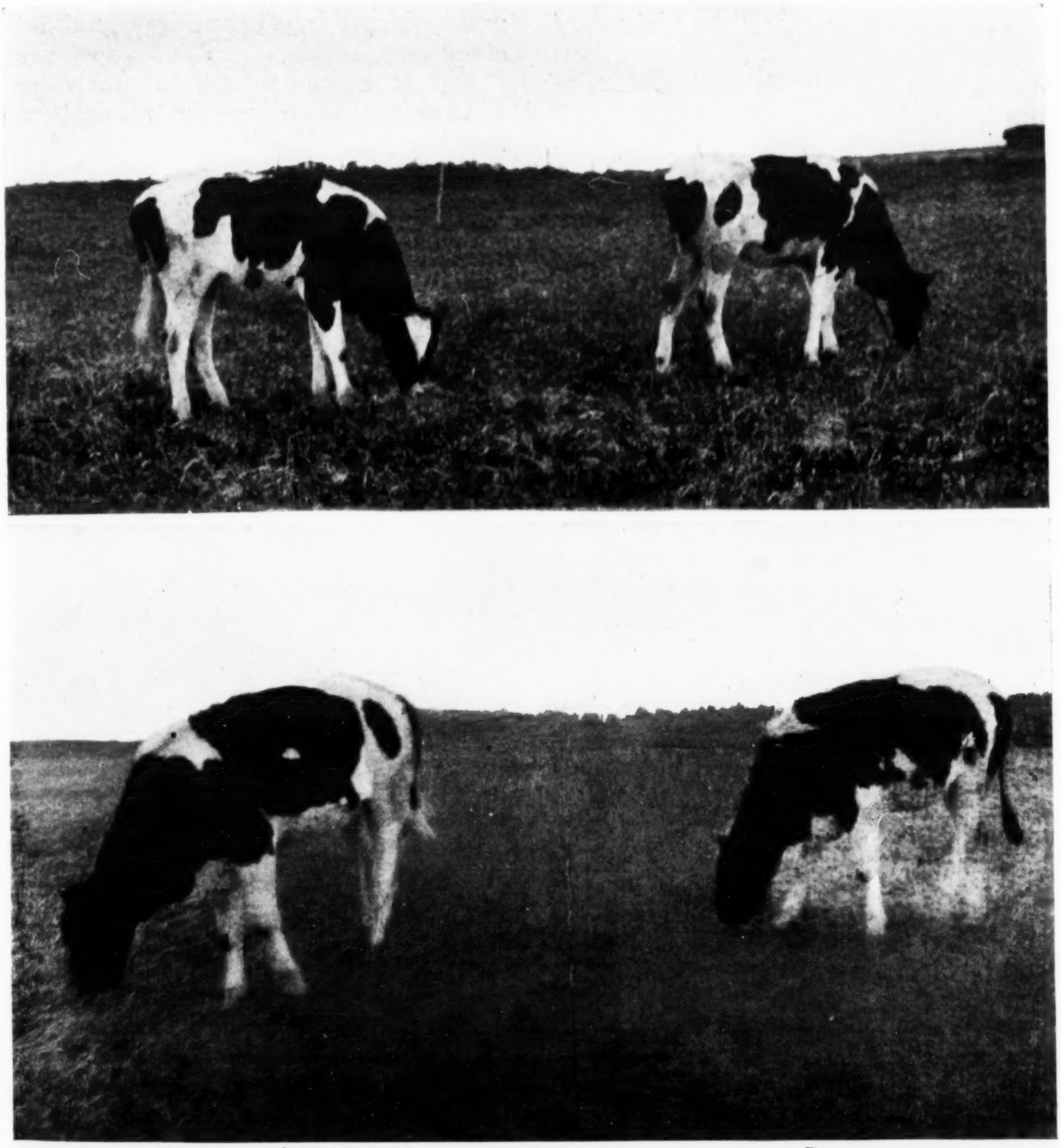
Mirror-imaging is certainly not found in all conjoined monsters nor is it evident in more than a small percentage of monozygotic twins. Where present, however, it is, as Newman points out, a reliable indication of their common origin. This is the condition found in the two heifers of the quadruplets.

Photographs taken by the writer when the calves were a few days more than a year old illustrate a fairly clear case of mirror-imaging of their black and white markings. (Figures 2 and 3).

One is first struck with the similarity between the large black spot in the right lumbar region of *B* and that in the corresponding location on the left side of *A*. Both are in the same region, of approximately the same size and shape and both point in the same direction. This would not be significant if this particular region were one of the six centres from which, as Allen[1] has pointed out, pigment formation tends to spread in mammals and birds. This, however, is not the case. The large spot on the flank comes as a result of a "secondary break" in the large pleural (side) patch of black pigment. Allen's studies indicate that in cattle two secondary breaks tend to cut the pleural pigment patch into three regions, one just behind the shoulder, a second over the last ribs and the third in the lumbar region. In this case the lumbar area has been entirely cut off and appears as a separate patch.

A similar secondary break in the pleural patch is evident on the left side of *A* and on the right side of *B* but in neither case has it progressed as far as on the opposite sides of these animals. It is of almost the same extent in both cases but this is partially obscured by a small spot of black pigment which has slipped down into the secondary break of *B* (right side) whereas this break is unspotted in *A* (left side).

Marked similarity is also evident between the lower margins of the side



A B

MIRROR IMAGE PATTERNS

Figure 3

The two heifers, *A* and *B*, considered monozygotic, from the right side, (above), and from the left side, (below). Note that the right side of *A* resembles the left side of *B*, and vice versa. This mirror image relation of the patterns is strong evidence that the heifers are identical twins.

patch on the right of *A* and that on the left of *B*. Both tend to run to a point and both have a small spot of black isolated from the main pigmented area at about the same point. The resemblance of these two sides arises from the "primary break" between side and shoulder patches being of approximately the same extent in both cases although it is less so on the dorsal margin than on the ventral one. On these same sides the shoulder patch extends down on the leg to the same extent in both cases although more anteriorly in *B* than in *A*.

The pleural patch on the right of *B* terminates ventrally in a spot well down on the flank. This is copied on the left flank of *A*.

The pigmented areas of the shoulder and neck centres overlap to some extent in these two animals so that a sharp division between them is not evident. However, from one or both of these patches there is produced an extension on the right fore-leg of *B* which closely resembles in shape and location the corresponding extension on the left fore-leg of *A*—more so than either of these patches resembles that on its own opposite side. At the dorsal margin a narrow primary break is evident between the neck and shoulder patches on the right side of *B*. The same break is quite evident at the ventral margin in the left of *A*, but, though present, it does not stand out at the dorsal surface as in *B* because the shoulder patch,—already small in *B*—has disappeared there in *A*.

The case for mirror-imaging may be summed up by saying that the right side of *A* resembles the left side of *B* more closely than it does *A's* own left side and, conversely, the left of *A* is more like the right of *B* than like *A's* own right.

There are small differences, it is true. However, white spotting is one of the most variable of characters and apparently one that is much influenced by irregularities in development. Kröning's investigation (*loc. cit.*) shows conclusively that there may be great differences between the colour patterns of individual members of conjoined monsters which, *ipso facto,* must be genotypically identical. This same fact has also been demonstrated in another way by Wright[25] who, working with guinea pigs, found that even after 20 generations of close inbreeding, when a family had been reduced almost to a pure line, the amounts of white spotting exhibited by litter mates might range anywhere from 20 to 90 per cent. The close mirror-imaging of the right and left sides of the two heifers described above is therefore all the more remarkable because of the natural variability of the white spotting character.

Wright calculated that in members of such highly inbred families the variations in pattern were determined about 3 per cent by heredity, 5 per cent by tangible environmental factors and 92 per cent by irregularities in development. One cannot argue that the same conditions apply to ungulates as to rodents, but even if they do so only in part, the close resemblance of the sides compared above indicates that both animals were exposed to remarkably similar intrauterine conditions. This could occur most easily if both were in the same horn of the bicornuate uterus and if both were enclosed in the same chorion. Evidence is given below that these two conditions, which, of course, would be expected in monozygotic twins, were present.

It should be pointed out also that the extent of the black colour in each of the primary pigment areas,—aural, nuchal, scapular, pleural and sacral (Allen[1])—is essentially the same in both calves. The bull and the freemartin differed greatly in this respect and similar differences are apparent in the several pairs of Holstein twins illustrated in previous numbers of this journal.[8, 16]

It is significant also that the triangular white blaze and the amount of white on the muzzle are practically identical in the two heifers. (Figure 2). In the heads of ten bovine monsters illustrated by Kröning[11] there is a wide range of markings such as is seen in any Holstein-Friesian herd, but between the two heads on any one monster there is in most cases a remarkably close resemblance such as is shown by the two animals herein compared. The bull and freemartin of these quadruplets appear at first

glance to be alike in this respect but the latter has much more white on the sides of the face.

Breeding Behaviour

Unfortunately the writer was unable at the time these calves were first seen to take measurements or to make a more detailed examination of their resemblance. On his return to Brandon after being away from Manitoba over a year it was found that one of the heifers had turned out to be a "shy breeder" and had therefore been slaughtered. Further comparisons were thus made impossible but through the courtesy of Mr. W. E. Lawson, Sheriff M. McGregor and Dr. Harry Ross, considerable additional data were obtained through correspondence and on the occasion of a visit to Brandon in the summer of 1929.

The two heifers came in heat at 10 months and 12 days but neither of them ever became pregnant. The butcher who dressed the carcass of one of the heifers informed the writer that its reproductive organs were not normal and were in some respects like those of the free-martin of the quadruplets, which he had also dressed. It is unfortunate that a detailed and accurate description of the anatomy of the reproductive system could not have been obtained. The other heifer changed owners twice but Dr. Ross has reported that it had never been in calf. One cannot say definitely that these two heifers were free-martins and that they had been made so through the usual medium of the testicular hormone from the bull calf but this is the most probable explanation.

The bull has sired a few calves. This indicates that the mechanism of hormone action whereby free-martins are produced is not a reversible reaction which can be upset by altering the *amounts* of the male and female hormones. In other words one bull calf produced enough testicular hormone to affect seriously the reproductive systems of the three females, but although there were apparently vascular connections between the bull and all three heifers, the combined endocrine secretions of the latter were unable to affect the reproductive system of the bull. This is in accord with the conclusions of Lillie[13] and of Bissonnette[4] that the modification of the female by the hormones of the male is an all-or-none reaction, dependent for the intensity of its action upon the time of onset of the testicular hormone rather than upon any quantitative differences in the two conflicting forces.

Position of the Calves *in Utero*

Dr. Ross, who removed the placentae, writes that "the foetal envelopes were three." This was to be expected if two of the four calves were monozygotic, but it cannot be taken as proof positive because of the tendency, observed by Lillie,[12] for chorions to fuse in cases of dizygotic twinning. However, the fact that there were only three sets of foetal envelopes is especially significant when considered along with the birth order, which was—bull, heifer, heifer, free-martin.

It is obvious that the bull, born first, must have been at the base of one of the two horns of the uterus, and that the free-martin, born last, must have been nearer the tip of one of the horns. It was to be expected that the two heifers would be born consecutively if they were monozygotic, since both would be enclosed in the same chorion (even possibly in the same amnion) and its rupture would facilitate the birth of the second twin right after that of the first. On the other hand it must be pointed out that had there been four chorions instead of three, even if the two were dizygotic twins, their consecutive birth could be expected in twelve cases out of the twenty-four possible

ways in which the births of the four calves might then have been arranged. However, there were only three chorions and it seems most probable that whatever two of the four animals were in one common chorion would be born consecutively. On this basis, and considering the birth order, the most logical interpretation is that the bull and the free-martin were in separate chorions in one horn of the uterus while the two heifers were in the other horn.

If this were not the case, there must have been one of the heifers in the same horn as the bull which would mean that the other heifer must have been between the bull and the free-martin since the latter could only have been near the tip of one horn. In such a condition it is impossible to see how the free-martin, being furthest away, could be so much more affected than the heifer between it and the bull, since the opportunity would obviously be greater for vascular anastomosis between the chorions of the bull and the adjacent heifer than between those of the bull and the more remote free-martin. This alternative is therefore untenable and the original premise that the two heifers were in one horn and presumably in a common chorion seems the more logical interpretation. As pointed out previously, such a condition would be expected if the two were monozygotic and would almost be necessary in addition to genotypic identity to bring about the close resemblance in colour pattern of the sides to which, by the separation of the original primordia of right and left sides of one animal, there had been conveyed the genetic potentialities for identical patterns.

The fact that the free-martin was obviously more affected by the testicular hormone than were the two heifers also suggests that it and the bull were in one horn since such an arrangement would facilitate an earlier anastomosis of chorionic blood vessels, which, in turn, would permit the maximum effect of the hormone from the bull. Conversely, one would expect less effect (as was evident) upon the two calves in the opposite horn because of the opportunity for vascular anastomosis between their chorion and that of the bull being delayed longer than if both chorions were in the same horn.

The greater degree of abnormality exhibited by the free-martin compared with that of the two heifers, and the fact that both of the latter were apparently affected to the same extent (since both came in heat at the same time, appeared normal and were not considered free-martins till found to be shy breeders) are quite easily explained by the evidence from Lillie's work that the modification of the free-martin is an "all or none" reaction, varying in degree according to the time of onset of the testicular hormone, and by the two heifers being in a common chorion in the same horn of the uterus. There is still the possibility that this common chorion may have arisen from the fusion of two separate membranes, but in view of the other evidence for the two animals being monozygotic, this seems less likely.

A necessary corollary to the arrangement of the four calves *in utero* suggested above is that, while there must have been a fusion of the chorions of the bull and the free-martin sufficient to permit vascular anastomosis, such a fusion should not have been extensive enough to prevent them being recognized upon removal as two distinct chorions, comprising two of the three sets of foetal envelopes mentioned by Dr. Ross. A survey of the literature reveals nothing to indicate that a bull and a free-martin must necessarily be enclosed in a single chorion.

Weights

The only weights available were taken when the calves were 13 days of age. They were recorded as follows:

Bull	72½ lbs.
Heifer	63 lbs.
Heifer	60½ lbs.
Heifer	59½ lbs.

Dr. Ross writes that the free-martin was the heaviest of the three heifers. This would mean that the two considered monozygotic weighed within one pound of each other at 13 days. Such a close agreement at that age is even more significant than if it had been observed in the weights at birth.

Discussion

The rarity of monozygotic twins in cattle has been discussed by Lillie,[12, 13] Gowen[6] and other writers, some of whom have expressed doubt whether such twins ever occur. While it is true that a case of monozygotic bovine twins has not yet been demonstrated to the satisfaction of all biologists; nevertheless it has not yet been shown that such an event may not occur.

The best embryological evidence for monozygotic twinning is the finding of only one corpus luteum in both ovaries of a cow carrying twin embryos. Out of 126 cases of twin bovine embryos, where both ovaries were examined by Keller and Tandler (cited from Lillie), or by Lillie,[13] one instance was found by the latter in which only one corpus luteum was present. This must have been a case of monozygotic twinning unless the Graafian follicle had liberated two ova.

Pearl[19] has suggested that two of the triplet calves described by him might be monozygotic. Lush[14] has described and pictured twin bull zebus (*Bos indicus*) which were so alike in conformation and markings that they might be considered identical and twin Jerseys[15] which from the standpoints of colour, conformation, breeding behaviour and milk yield seemed almost certainly identical. It seems possible that although monozygotic bovine twins are quite rare, other cases could be brought to light and definitely established if veterinarians, animal husbandmen and others who have frequent opportunity to observe twin calves would attempt to get evidence from every angle bearing on the case. Such studies would be facilitated if a means could be found to distinguish between a chorion originally single and one arising from the fusion of two separate chorions. Reichle[20] has recently pointed out that in man such a distinction is possible by examination of the septum to see if chorionic tissue be present between the two amniotic layers. Whether or not the same distinction can be made in bovine birth membranes has not yet been proved.

It is probable that cases of monozygotic twins will be more easily recognized in breeds exhibiting white spotting such as the Holstein-Friesian, Guernsey and Ayrshire, than in self-coloured breeds. It should be pointed out, however, that from analogy with twins in man, reversed asymmetry, or mirror imaging, such as has been described in this paper, is to be expected less frequently than cases where the right side of one twin resembles the right side of the other, with similar correspondence being shown in the two left sides.

Apart from the biological interest attached to bovine monozygotic twins, such animals would be particularly valuable for investigations in nutrition, physiology and husbandry because of their being genotypically identical. A feeding experiment repeated upon each animal and using first one twin and then the other as a control would probably yield more conclusive results than if a dozen animals of greater genetic heterogeneity and of different ages were used for the same test.

Summary

A case of living bovine quadruplets is reported in which there were one bull, one free-martin and two heifers which, being sterile, were probably also free-martins affected to a lesser degree than their "litter" sister. All four animals lived to breeding age. The bull produced a few calves.

The two heifers least affected exhibited reversed asymmetry or mirror-imaging in their black and white colour patterns. They were practically identical in facial markings. Their weights at thirteen days varied only half a pound from the average of the two. From the birth order and foetal membranes of the quadruplets it is most probable that the two heifers were enclosed in a common chorion in one horn of the uterus.

In view of all these facts, it is considered that the two heifers constitute an authentic case of so-called "identical" or monozygotic twinning in cattle.

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THE GENETICAL THEORY OF NATURAL SELECTION

A Review

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DURING the latter part of the nineteenth century, increasing difficulty was felt in accepting Darwin's conception of the evolutionary process as one in which variation merely plays the subordinate (though necessary) rôle of providing a field of potentialities, through which the actual direction of advance is determined by natural selection. Theories were developed according to which the "origin of species" was to be sought more directly in the "origin of variation." Most of these were Lamarckian, others, of which de Vries' theory was most important, were not. The rediscovery of Mendelian heredity was a direct consequence of the mutation theory of the origin of species and was naturally seized upon as supporting this view. Only gradually has it become apparent that the real implications of Mendelian heredity are exactly the opposite and that in fact, it supplies the answer to some of the main difficulties felt with Darwin's theory. Dr. Fisher has played a leading part in developing the statistical consequences of Mendelian heredity and here brings together his views in a unified form.* It is a book which is certain to take rank as one of the major contributions to the theory of evolution.

The first chapter is concerned with a comparison of the consequences of blending and particulate heredity. A consequence of blending heredity, which Dr. Fisher shows was well understood by Darwin, and which was felt by him, and others, as a major difficulty with his theory, is the fact that under such heredity, the variability of a population tends to be greatly reduced in each successive generation. The portion of the variance lost per generation is one-half (if there is no assortative mating) and after ten generations only one-tenth of one per cent is left. Thus Darwin felt constrained to believe that an enormous amount of new variation appears in each generation, the differences among brothers being of this sort. This variability must be seized upon at once by natural selection or it will be lost. With even a slight departure from randomness in its occurrence, direction of mutation, rather than natural selection becomes the guiding principle of evolution.

All of this was changed with the demonstration of particulate inheritance and orderly segregation. The frequencies of zygotes of the types *aa*, *Aa* and *AA* tend to remain indefinitely in the proportions of a binomial square $p^2+2pq+q^2$ where p and q are the proportion in which alternative genes are represented in the population. In a population of limited size, to be sure, there is some variability of gene frequency, due to the accidents of sampling from generation to generation, but this brings about only a very low rate of reduction of variance. As to the actual rate of reduction of variance (and of heterozygosis), Fisher here confirms the figure which I had obtained by the method of path coefficients, viz. $\frac{1}{2n}$ per generation, where n is the effective size of the breeding population. The modern geneticist may get an appreciation of the difficulties which confronted

*The Genetical Theory of Natural Selection, by R. A. Fisher Sc. D., F. R. S., Price $6.00. Oxford University Press, New York. 1930.

Darwin, in attempting to account for natural variability and to apply selection as a guiding principle, by considering the case of a self-fertilized line, in which the loss of variance actually is 50% per generation, the same as with a random breeding population under blending heredity. The difference that with any initial variability, the inbred line tends to split up into many diverse lines, while the population under blending heredity becomes fixed as of one type , further emphasizes the difficulty. That pure lines actually show very little genetic variability, Fisher points out, is convincing evidence that substantially all inheritance is Mendelian. A quotation will bring out his conclusions with regard to mutation and selection:

> For mutations to dominate the trend of evolution it is thus necessary to postulate mutation rates immensely greater than those which are known to occur and of an order of magnitude which in general would be incompatible with particulate inheritance. * * * The whole group of theories which ascribe to hypothetical physiological mechanisms, controlling the occurrence of mutations, a power of directing the course of evolution, must be set aside once the blending theory of inheritance is abandoned. The sole surviving theory is that of natural selection and it would appear impossible to avoid the conclusion that if any evolutionary phenomenon appears to be inexplicable on this theory it must be accepted at present merely as one of the facts which in the present state of knowledge seems inexplicable.

I may state at this point that I am in accord with Dr. Fisher on the rôle of mutation, except that I would perhaps allow occasional significance to chromosome aberration, and to hybridization, as direct species forming agencies. It appears to me, however, that in this statement and throughout the book, he overlooks the rôle of inbreeding as a factor leading to nonadaptive differentiation of local strains, through selection of which, adaptive evolution of the species as a whole may be brought about more effectively than through mass selection of individuals.

Distribution of Gene Frequencies

The central problem in the analysis of the statistical consequences of Mendelian heredity is that of determining the distribution of gene frequencies under the pressures of mutation, selection, migration, etc., and not least important, as affected by size of population. Under given conditions, what proportion of the genes will be fixed? How many will have frequencies in the neighborhood of 50%? How many 99%? How rapidly will new mutations attain fixation under favorable selection? Two of the chapters (IV, V), are devoted to a mathematical investigation of such questions. As I have recently presented certain results in this field,* it may be of interest to bring out the points of agreement and disagreement.

My approach to the subject was from a different angle than Dr. Fisher's in being through the problem of inbreeding. I found that the decrease in heterozygosis, to be expected under inbreeding (but ignoring new mutations and selection) could be obtained by an application of the method of path coefficients.[4] The method could be applied to complex pedigrees encountered in livestock, and studies of the history of the Shorthorn breed of cattle have been made by means of it by Dr. McPhee and myself[5] of Clydesdale horses by Calder,[1] and of Jersey cattle by Buchanan Smith.[3] In the case of random mating in a population of N_m males and N_f females, it gave as a close approximation $\frac{1}{8N_m}+\frac{1}{8N_f}$ as the rate of loss of heterozygosis (and hence of variance) per generation. With an equal number of males and females in a total breeding population of n this reduces to the $\frac{1}{2n}$ referred to above. Fisher, studying the problem of evolution of large popula-

*These results were presented at the 1929 meeting of the A. A. A. S. An abstract appeared in the *Anatomical Record* (Vol. 44, p. 287, 1929). The full paper is to appear in *Genetics*.

tions, made the first attempt to find the actual distribution of gene frequencies under various conditions.[2] He reached a solution for the case of unselected genes not replenished by mutation, which indicated loss of variance at the rate of $\frac{1}{4n}$ per generation, just half of the rate indicated by my method. His formula for the distribution of gene frequencies was expressed on a scale of the logarithms of the ratio of alternative gene frequencies $\log\frac{q}{1-q}$, a scale which has the advantage of stretching the important regions close to 0% and 100% and also of making the effect of simple selection uniform at all points. It is interesting to note, however, that on transforming his formula to the simple scale of percentage frequencies it indicates an equal number of genes at all frequencies ($y = 1$). He also obtained a solution for the case in which decrease in heterozygosis is just balanced by mutation.

On noting the discrepancy between his result and mine for decrease in the rate of heterozygosis, I was not able to correct a questionable point in his derivation, but was able to reach a formula for the distribution of gene frequencies in a different way. The result agreed with his solution in form ($y = 1$), but with the rate of decline as $\frac{1}{2n}$ per generation. In the case of loss of variance, balanced by mutation, the distribution differed considerably in form, being $y=\frac{1}{2n[.577+\log(2n)]q(1-q)}$ instead of his $\frac{1}{\pi\sqrt{q(1-q)}}$. It appeared further from this method that a selective advantage such that genes A and a reproduce in the ratio $1:1-S$ introduced an exponential term e^{2ns} into the formula. This is valid, however, only for irreversible mutation and then only for extremely small values of the selection coefficient. It now appears that for reversible mutation and in any case for values considerably larger than $\frac{1}{2n}$ it should be e^{4ns}. Appreciable rates of recurrence of mutation (u) and reverse mutation (v) were stated* to throw the formula into the form $y=Cx^{4nv}q^{4nu-1}(1-q)^{4nv-1}$ a curve which for high mutation rates (relative to $\frac{1}{2n}$) approaches the form of a probability curve and indicates a random drifting of gene frequency about an equilibrium point. The case which has seemed most important to me is that of the effects of migration in a population which is a sub-group of a large one. The formula is similar mathematically to that for mutation. It is given below in a revised form.

These results were communicated to Dr. Fisher, who now finds on re-examination of his method, that the addition of a term which had seemed unimportant gives a confirmation of my formulae in the first two cases. He obtains on the other hand, a somewhat different form for the effect of selection, viz., $y=\frac{s}{pq}\left(\frac{1-e^{-4ms}}{1-e^{-4Ns}}\right)$ where his a is my s, except for a change of sign. The exact case which he deals with, is not one which I had considered, a fact which reflects our differences in viewpoint on the general problem. His formula refers to flux equilibrium with respect to an inexhaustible supply of irreversible mutations. On solving for it by my method I get results substantially identical with his as long as the selection coefficient is less than $\frac{1}{2n}$. Above this there is rapid divergence. His formula is undoubtedly a better approximation, and in fact, I may say that on reexamination, I find that I, in turn, have here neglected terms which should be taken account of. The general formula for a partially isolated population by my method, as now revised, is as follows: $y=Cx^{4Ns}q^{4N(mq_m+v)-1}(1-q)^{4N[m(1-q_m)+u]-1}$ where m is the rate of population exchange with the species as a whole, q_m is the gene frequency in the latter and s measures the differential selection of the group as compared with the species as a whole. If v is actually zero (completely irreversible mutation from an inexhaustible supply of genes), and no im-

*Presented without proof in *American Nat.* 63:556-561 (1929).

migration is assumed, the formula takes a somewhat different form and in fact reduces to Dr. Fisher's result, identically. Summing up, our mathematical results on the distribution of gene frequencies are now in complete agreement as far as comparable, although based on very different methods of attack. He has not yet checked my conclusions as to the effects of recurrent and reversible mutation and of immigration by his method.

Differences in Interpretation

There are, however, important differences in interpretation. Dr. Fisher is interested in the figure $\frac{1}{2n}$, measuring decrease in variance, only because of its extreme smallness, from which he argues that the effects of random sampling are negligible in evolution (except as bearing on the chances of loss of a recently originated gene). I, on the contrary, have attributed to the inbreeding effect, measured by this coefficient, an essential rôle in the theory of evolution, arguing that the effective breeding population, represented by n of the formula may after all be relatively small compared with the actual size of the population. In this view I have been encouraged by the rather high coefficients of inbreeding found even in entire breeds of livestock. Calder, for example, finds a rate of increase of the inbreeding coefficient in Scotch Clydesdale horses of nearly 1% per generation which let it be emphasized again is a direct determination of the value of $\frac{1}{2n}$ for this large breed, assuming as seems to be justified, that there is no important subdivision into local strains.

The core of Dr. Fisher's theory of selection is given in Chapter II. He reaches a formula on which he lays great emphasis as "the fundamental theorem of natural selection." "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time." This is given as exact for idealized populations in which fortuitous fluctuations in genetic composition have been excluded *i. e.*, in indefinitely large populations. He calculates the standard error of the rate of advance in fitness, due to such fluctuations, and concludes that this is negligibly small; even over a single generation, in populations of the order of size of natural species. This means that the small random fluctuations in the frequencies of individual genes balance each other in their effect on a selected character to such an extent that irregularities in evolutionary advance are of the second order with respect to the rate of advance. He compares this principle to the regular increase of entropy in a physical system. The only effective offset to undeviating increase in fitness, which he recognizes, is change of environment, living or non-living, which he points out must usually be for the worse. The net effect of natural selection, and change of environment is registered in an increase or decrease in numbers and a somewhat winding course of evolution.

The splitting of species, he attributes to differences in the direction of selection in different parts of the range. The process may be facilitated by geographic (or other) isolation, but he holds that it may also be brought about wholly by selection, the primary selection tending to set up secondary processes (including especially preferential mating *i. e.*, sexual selection), which in the end may lead to complete fission of the species.

It will be seen that Dr. Fisher's conception of evolution is pure Darwinian selection. The extent to which he carries the principle is well illustrated in his theory of dominance (chapter III) in which he attempts to account for the prevalent dominance of type genes, over mutant genes by the natural selection of modifiers of dominance.* I

*This theory was first elaborated by Fisher in papers which appeared in *The American Naturalist* (62:115-126, 571-574, 1928). In a criticism of it (*American Naturalist* 63:274-

have pointed out elsewhere and he has agreed, that the selection pressure on the modifiers is here of the second order, compared with the rate of mutation of the primary gene. It seemed probable to me that such a minute selection pressure would ordinarily be of the second order compared with other selection pressures acting on the same gene, and therefore negligible. Dr. Fisher on the other hand, adheres to the effectiveness of selection in this case.

In order to bring out the point at which we part company with respect to the efficacy of selection, it will be necessary to return to Dr. Fisher's fundamental theorem: "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time." One's first impression is that the genetic variance in fitness must in general be large and that hence if the theorem is correct the rate of advance must be rapid. As Dr. Fisher insists, however, the statement must be considered in connection with the precise definition which he gives of the terms. He uses "genetic variance" in a special sense. It does not include all variability due to differences in genetic constitution of individuals. He assumes that each gene is assigned a constant value, measuring its contribution to the character of the individual (here fitness) in such a way that the sums of the contributions of all genes will equal as closely as possible the actual measures of the character in the individuals of the population. Obviously there could be exact agreement in all cases only if dominance and epistatic relationships were completely lacking. Actually, dominance is very common and with respect to such a character as fitness, it may safely be assumed that there are always important epistatic effects. Genes favorable in one combination, are, for example, extremely likely to be unfavorable in another. Thus allelomorphs which are held in equilibrium by a balance of opposing selection tendencies (possibilities of which are discussed in Chapter V) may contribute a great deal to the total genetically determined variance but not at all to the genetic variance in Fisher's special sense, since at equilibrium there is no difference in their contributions. The formula itself seems to need revision in the case of another important class of genes, ones slightly deleterious in effect but maintained at a certain equilibrium in frequency by recurrent mutation (or migration). These contribute to the genetic variance of the species, but not to the increase in fitness. Terms involving mutation (and migration) rates seem to be omitted in the formula as given.

Mutational Flux as a Factor

Consider now the case of a population so large that fortuitous variation of gene frequency is negligible. According to my view, such a population is one in which all mutations which can occur will recur at measurable rates. All genes which are not fixed will be held in equilibrium by opposing selections, or by selection opposed by mutation, the cases just discussed. Thus while there may be a great deal of genetically determined variance, there will be no movement of gene frequencies and hence no evolution as long as external conditions remain constant. This state of equilibrium may be upset by change of external conditions, bringing changes in the direction and intensity of selection. All gene frequencies may then be expected to shift in an orderly fashion until the equilibrium consistent with the new conditions is attained. On return to the old conditions, all gene frequencies should shift back to the old positions. It may be granted that an irregular sequence

297, 1929). I proposed an alternative directly physiological interpretation of the phenomenon. Further discussion may be found in Fisher's reply to this criticism (*American Naturalist* 63:553-556, a counter-reply *ibid* 556-561 and a paper by J. B. S. Haldane, *American Naturalist* 64:87-90 1930).

of environmental condition would result occasionally in irreversible changes (because of epistatic relationships) thus giving a real, if very slow, evolutionary process; but this is not Dr. Fisher's scheme under which evolution should proceed under constant external conditions. He would have the system of equilibria of gene frequencies kept in motion by a steady flux of novel mutations. These to be effective must be advantageous practically from the first, since non-recurrent, unfavorable mutations would be lost (in an indefinitely large population) before they could reach such a frequency as to have any appreciable effect on the situation. Even those advantageous at once would also usually be lost within a few generations of their appearance. They would, however, as Dr. Fisher shows, have a finite chance of reaching high frequencies and ultimately fixation. In their progress, they may be expected to unsettle the equilibria of other genes by creating new favorable (or unfavorable) combinations. Thus the entire system of gene frequencies is thrown into motion and may yield the steady adaptive advance of the theory.

As noted above, this scheme appears to depend on an inexhaustible flow of new favorable mutations. Dr. Fisher does not go into this matter of inexhaustibility but presumably it may be obtained by supposing that each locus is capable of an indefinitely extended series of multiple allelomorphs, each new gene becoming a potential source of genes which could not have appeared previously. The greatest difficulty, seems to be in the posited favorable character of the mutations. Dr. Fisher, elsewhere, presents cogent reasons as to why the great majority of all mutations should be deleterious. He shows that all mutations affecting a metrical character "unless they possess countervailing advantages in other respects will be initially disadvantageous." He shows that in any case the greater the effect, the less the chance of being adaptive. Add to this the point that mutations as a rule probably have multiple effects, and that the sign of the net selection pressure is determined by the greater effects, and it will be seen that the chances of occurrence of new mutations, advantageous from the first are small indeed.

Partial Isolation as a Factor

I would not deny the possibility of very slow evolutionary advance through this mechanism but it has seemed to me that there is another mechanism which would be much more effective in preventing the system of gene frequencies from settling into a state of equilibrium, than the occurrence of new immediately favorable mutations. If the population is not too large, the effects of random sampling of gametes in each generation brings about a random drifting of the gene frequencies about their mean positions of equilibrium. In such a population we can not speak of single equilibrium values but of probability arrays for each gene, even under constant external conditions. If the population is too small, this random drifting about leads inevitably to fixation of one or the other allelomorph, loss of variance, and degeneration. At a certain intermediate size of population, however (relative to prevailing mutation and selection rates), there will be a continuous kaleidescopic shifting of the prevailing gene combinations, not adaptive itself, but providing an opportunity for the occasional appearance of new adaptive combinations of types which would never be reached by a direct selection process. There would follow thorough-going changes in the system of selection coefficients, changes in the probability arrays themselves of the various genes and in the long run an essentially irreversible adaptive advance of the species. It has seemed to me that the conditions for evolution would be more favorable here than in the indefinitely large population of Dr. Fisher's scheme. It would, however, be very slow, even in terms of geologic time, since it can be shown to be

limited by mutation rate. A much more favorable condition would be that of a large population, broken up into imperfectly isolated local strains. The probability array for genes within such a local strain has been given on a previous page. The rate of evolutionary change depends primarily on the balance between the effective size of population in the local strain (n) and the amount of interchange of individuals with the species as a whole (m) and is therefore not limited by mutation rates. The consequence would seem to be a rapid differentiation of local strains, in itself non-adaptive, but permitting selective increase or decrease of the numbers in different strains and thus leading to relatively rapid adaptive advance of the species as a whole. Thus I would hold that a condition of subdivision of the species is important in evolution not merely as an occasional precursor of fission, but also as an essential factor in its evolution as a single group. Between the primary gene mutations, gradually carrying each locus through an endless succession of allelomorphs, and the control of the major trends of evolution by natural selection, I would interpolate a process of largely random differentiation of local strains. As to the existence of such strain differences, the situations described in the herring by Heinke, in Zoarces and Lebistes by J. Schmidt, and in deer mice by Sumner, as well as the situation in man, may be called to mind.

Sexual Selection and Mimicry

To the general biological reader, the later chapters of the book dealing with concrete applications of the selection principle may prove most attractive. A well sustained attempt to rehabilitate Darwin's theory of sexual selection has already been noted. Another chapter deals with mimicry. The validity of both Batesian and Müllerian mimicry is accepted and the possibility of accounting for the origin of each sort by natural selection is developed after careful analysis of opposing arguments which have been widely accepted, especially in the case of Müllerian mimicry. The author naturally applies his theory of direct progress through mass selection. It appears to me, however, that these cases fall at least equally well under the viewpoint which I have developed, which does not require such a minutely continuous path of selective advantage between the original pattern of the species and that ultimately reached.

Evolution In Man

More than one-third of the book is devoted to discussion of the trend of evolution in man. This portion deserves the most careful consideration by all interested in problems of Eugenics. The course of the argument may be summarized briefly as follows: One might expect to find that civilization once started on the earth would give such an advantage that its history would be an uninterrupted succession of triumphs. Instead of this, we find that every civilization, after a period of prosperity, has fallen into decay, and succumbed to the onslaughts of numerically weak, barbarous peoples. The cause of this decay, he finds reason to believe, is genetical rather than social. Evidence indicates that differences in fertility are in part hereditary, whether dependent on physical or mental qualities. The bulk of the evidence from civilized communities, ancient and modern, indicates that fertility is lowest in the upper classes of the population, where qualities which make for individual ability and leadership are most frequent. The reason for this inversion of the normal relation is seen in the tendency (first pointed out by Galton) for infertility as well as ability to rise in the social scale. The result is a tendency to extinction of ability, applying to all classes in society. Examination of conditions in more primitive societies organized on the clan basis, lead to the conclusion that the play of natural selection is here exactly the op-

posite. The evolution of individual qualities he believes reaches its climax just before civilization begins.

The final chapter deals with the conditions necessary for a permanent civilization. The author holds that only a wage system definitely designed to remove the present severe social penalty on fertility and indeed tending to promote fertility would adequately oppose the present tendency toward racial deterioration.

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Books Received

BOOKS are acknowledged in this column as received, and such acknowledgment must be regarded as sufficient return for the courtesy of the sender. As far as space permits, books that contain material of special interest to the readers of the Journal *will be reviewed in later numbers.*

THE DRIFT OF CIVILIZATION, A Symposium. *By* the Contributors (26) to the Fiftieth Anniversary Number of the St. Louis Post-Dispatch, including Albert Einstein, J. B. S. Haldane, Maxim Gorky, Sir Philip Gibbs, Wm. Howard Taft, Richard E. Byrd, etc. Pp. 268. 26 Chapters. Price, $3.00. Simon and Schuster, New York. 1929.

The title of this book is symptomatic. How long are we going to be content to trust the progress of civilization to so casual a process as drifting?

SCIENCE IN SOVIET RUSSIA, *by* J. G. Crowther. Pp. 128. 27 Chapters. Price, 7s.6d. Williams & Norgate, Ltd., London. 1930.

THE RETREAT FROM PARENTHOOD, *by* Jean Ayling. Pp. 293. 33 Chapters. Price, 10s.6d. Kegan Paul, Trench, Trubner & Co., Ltd., London. 1930.

The latest birth statistics indicate the retreat has become a rout. If it continues so, can the drift of civilization continue in any direction but the vertical, and *not up*?

THE ENLARGEMENT OF PERSONALITY, Behavior Patterns and their Formation. *By* J. H. Denison. Pp. 340. 15 Chapters. Price, $3.00. Charles Scribner's Sons, New York. 1930.

One wonders—has too much enlargement of too many personalities contributed to the drift, and to the rout?

PROBLEMS OF MENTAL DEFICIENCY. Four Pamphlets: (1) Inheritance of Mental Defect, *by* Ulrich A. Hauber, Ph.D. (2) Social Care of the Mentally Deficient, *by* Charles Bernstein, M. D. (3) Moral Aspects of Sterilization, *by* John A. Ryan, D. D. (4) Eugenic Sterilization in the Laws of the States, *by* Wm. F. Montavon. Price, 10c each, or 25c for the series. National Catholic Welfare Conference, Washington, D. C. 1930.

One group that leaves its problems largely to others, and to whom the drift and the retreat mean little—"See the happy moron. He doesn't give a damn! I wish I were a moron. My God, perhaps I am!"

THE STHENICS, The Chord Invisible, *by* Sir James K. Fowler. Pp. 81. 11 Chapters. Price, $1.40. The Macmillan Co., New York. 1930.

CHRISTIANITY AND SEX, *by* Christopher Dawson. Pp. 40. Price, one shilling. Faber & Faber, London. 1930.

COMMITTEE FOR LEGALISING EUGENIC STERILIZATION. The Eugenics Society, England. Pp. 32. Price, 6d. The Eugenics Society, London. 1930.

A plea to make the retreat final, if not compulsory in case other means are hopeless.

(*Continued on page* 366)

THE PLANT PATENT LAW

(*Continued from the July* JOURNAL, *Page 322*)

Cooperation With Department of Agriculture

The bill proposes that the President may facilitate the administration of its provisions by the Patent Office through requiring the Secretary of Agriculture, to furnish the Commissioner of Patents with available information in the department, to conduct necessary research, and to detail to the Patent Office technical employees of the department. As to this feature the Secretary of Agriculture states in his letter set forth in Appendix A to this report that—

> As determination of the newness of varieties could not be made solely upon the basis of descriptive matter and drawings, it is evident that the specimens, photographs, paintings, descriptions, etc., of existing plants, already available in various forms in the Department of Agriculture and elsewhere, will be of great value, increased in due time by extension of such collections of plants and data.
>
> The effective administration of such legislation would require expert personnel, comparable in their lines, with the specialists now employed by the Patent Office. The technical personnel of the Department of Agriculture, although possibly inadequate to meet future demands, would be available in making such determinations as would be necessary in carrying out the purposes of such a law.

Application to Existing Plants

In accordance with existing patent law, the bill would not permit the patenting of plants that have been in public use, either before or after the approval of the bill, for more than two years. Furthermore, it was considered unnecessary to provide specifically that the bill shall permit the patenting of plants now in process of creation, under observation, under test, or in existence but not yet given to the public, as that appears to the committee to be covered adequately by the existing provisions of section 4886 of the Revised Statutes. With reference to plants, the words "public use" in that section would apply to the period during which the new variety is asexually reproduced for sale.

IV. Legal Phases of the Bill

The committee is of the opinion after careful consideration that the amendments to the patent laws proposed by the bill fall within the legislative power of Congress under Article I, section 8, of the Constitution—

> To promote the Progress of Science and useful Arts, by securing for limited Times to Authors and Inventors the exclusive Right to their respective Writings and Discoveries;

Present patent laws apply to—

> any person who has invented or discovered any new and useful art, machine, manufacture, or composition of matter, or any new and useful improvement thereof * * *.

It will be noted that the laws apply both to the acts of inventing and discovery and this alternative application has been true of the patent laws from their beginning. See, for instance, the patent act of 1790 (1 Stat. 109). The amendment proposed by the pending bill to care for plant patents likewise applies to "any person who has invented or discovered" the particular variety of plant.

There can be no doubt that the grant of plant patents constitutes a promotion of "the progress of science and useful arts" within the meaning of the constitutional provision. The only question is, Is the new variety a discovery and is the originator or discoverer an inventor?

There is a clear and logical distinction between the discovery of a new variety of plant and of certain inanimate things, such, for example, as a new and useful natural mineral. The mineral is created wholly by nature unassisted by man and is likely to be discovered in various parts of the country; and, being the property of all those on whose land it may be found, its free use by the respective owners

should of course be permitted. On the other hand, a plant discovery resulting from cultivation is unique, isolated, and is not repeated by nature, nor can it be reproduced by nature unaided by man, and such discoveries can only be made available to the public by encouraging those who own the single specimen to reproduce it asexually and thus create an adequate supply.

It is obvious that nature originally creates plants but it can not be denied that man often controls and directs the natural processes and produces a desired result. In such cases the part played by nature and man can not be completely separated or weighed or credited to one or the other. Nature in such instances, unaided by man, does not reproduce the new variety true to type.

Furthermore, there is no apparent difference, for instance, between the part played by the plant originator in the development of new plants and the part played by the chemist in the development of new compositions of matter which are patentable under existing law. Obviously, these new compositions of matter do not come into being solely by act of man. The chemist who invents the composition of matter must avail himself of the physical and chemical qualities inherent in the materials used and of the natural principles applicable to matter. Whether or not he is aware of these principles does not affect the question of patentability. The inventor of the composition of matter may have definitely in mind the new product and definitely worked toward it. On the other hand, as is true of many of the most important inventions, he may accidentally discover the product, perhaps in the course of the regular routine of his work. He does not have to show, for instance, that he mixed the elements and expected them to produce the particular composition of matter. He may simply find the resulting product and have the foresight and ability to see and appreciate its possibilities and to take steps to preserve its existence.

The same considerations are true of the plant breeder. He avails himself of the natural principles of genetics and of seed and bud variations. He cultivates the plants in his own laboratory under his own eye. He may test and experiment with them on a variety of proving grounds. He may promote natural cross-pollination by growing the parent plants in juxtaposition. For instance, because of manual difficulties artificial hand pollination is impracticable in the production of seed of the genus compositae, including such species as dahlias, chrysanthemums, asters, daisies, and the like, and also in the case of many of the small fruits. In other cases hand pollination is unnecessary; natural pollination does equally well. On the other hand, if the periods of the bloom of the plants differ hand pollination and the camel's-hair brush must be used. Again, orchids, avocados, grapes and most orchard fruits are subjected to hand pollination. In the case of sports, the plant breeder not only cultivates the plants but may subject them to various conditions of cultivation to encourage variation, as, for example, in some recent developments, the subjection of the plants to the effects of X-rays or to abnormal fertilization. Finally, the plant breeder must recognize the new and appreciate its possibilities either for public use or as a basis for further exercise of the art of selection.

Moreover, it is to be noted that the committee has, by its amendment in striking out the patenting of "newly found" varieties of plants, eliminated from the scope of the bill those wild varieties discovered by the plant explorer or other person who has in no way engaged either in plant cultivation or care and who has in no other way facilitated nature in the creation of a new and desirable variety.

But even were the plant developer's contributions in aid of nature less creative in character than those of the chemist in aiding nature to develop a

composition of matter which has theretofore been nonexistent (an assumption which the committee does not believe to have basis in fact and which is here made solely for purposes of argument), nevertheless the protection by patents of those engaged in plant research and discovery would not be beyond the constitutional power of the Congress.

At the time of the adoption of the Constitution the term "inventor" was used in two senses. In the first place the inventor was a discoverer, one who finds or finds out. In the second place an inventor was one who created someting new. All the dictionaries at the time of the framing of the Constitution recognized that "inventor" included the finder out or discoverer as well as the creator of something new. Thus Sheridan in 1790 defined "inventor" as "A finder out of something new," and "invention" as "discovery." Kersey in 1708 defined "invention" as "the act of inventing, or finding," and Martin in 1754 defined "to invent" as "to find out or discover." The word "discover" or "discovery" is given as an equivalent by Cocker in 1715 and 1724, Ash in 1775, Perry in 1795, Entick in 1786, Fenning in 1771, and Barclay in 1841. "To find" or "find out" or "finding" as a synonym of invent or inventor, was noted by Rider in 1617, Holy-oke in 1649, Coles in 1724, Johnson in 1824, Kendrick in 1773, Martin in 1754, Kersey in 1708, Sheridan in 1790, Ash in 1775, Cocker in 1715 and 1724, Entick in 1786 and 1791, Fenning in 1771, and Coxe in 1813.

The distinction between discovering or finding out on the one hand and creating or producing on the other hand, being recognized in the dictionaries current at the time of the framing of the Constitution, it is reasonable to suppose the framers of the Constitution attributed to the term "inventor" the then customary meaning. That they did not ignore the meaning of inventor as "a discoverer or finder out" is furthermore indicated by the fact that in the Constitution itself the framers referred to the productions of inventors as "discoveries."

With the development of the patent laws and modern industry the meaning of the word "inventor" as a creator of something new became the prevailing use and, while both meanings of inventor are still recognized in such modern dictionaries as Murray's New English Dictionary, Webster's New International Dictionary, and the Century Dictionary and Encyclopedia, the meaning of inventor as "a finder out or discoverer" is now considered obsolete or archaic. However, it seems to the committee that the meaning to be attached to the term "inventor" as used in the Constitution must be the meaning in general use at the time of the framing of the Constitution rather than the meaning prevailing in present-day usage.

Furthermore, there are many instances where the provisions of the Constitution have been held to embrace affairs which, while literally within the meaning of a constitutional phrase, were not conceived of by the framers at the time that the Constitution was written. For example, the power to regulate interstate commerce, which was then mainly by horse or by rowboat or sailboat, is now held by the courts to cover regulation of steam transportation, telegraphic communication, and even radio communication, matters beyond the wildest dreams of the framers of the Constitution.

An indication of the construction that the courts are likely to place on the word "inventor" in the constitutional provision can be found in their construction of the words "author" and "writer" in the same paragraph. The Constitution gives Congress power—

> To promote the Progress of Science and useful Arts, by securing for limited Times to Authors and Inventors the exclusive Right to their respective Writings and Discoveries.

Under this provision the original act of May 31, 1790 (1 Stat. 124), allowed copyright of maps and charts

as well as books. By successive legislation this right was extended to include photographs, statues, models, and designs. (See, for instance, 35 Stat. 1075.) It might well be doubted whether map makers, chart makers, photographers, sculptors, modelers, and designers were "authors," and whether maps, charts, photographs, statues, models, and designs were "writings," but the constitutionality of this legislation has been sustained from the beginning. Thus in Lithographic Co. *v.* Sarony (1883, 111 U. S. 53) it was contended that a photograph was not a writing nor the production of an author, but the Supreme Court sustained the statute allowing a copyright for photographs.

As to copyrights there was doubt on two words, "authors" and "writings," which certainly do not have in ordinary speech such broad meanings as Congress and the Supreme Court have given them. But the court had no difficulty in sustaining a sufficiently liberal construction. As to patents the doubt is only as to the one word, "inventors." The word "discovery" aptly describes the situation when a new and distinct variety of plant is found and "inventors" is certainly as elastic a word as "authors." It is not to be expected that the courts would place themselves in the position of impeding the progress of the science and useful art of agriculture by holding to so narrow a definition of the word "inventor" as to find that the proposed legislation was undoubtedly beyond the power of the Congress.

Appendix A—Letter of Secretary of Agriculture

[NOTE.—The letter of the Secretary of Agriculture is addressed to the proposed legislation as originally introduced as S. 3530 of the present session. As heretofore stated in the report, there are only minor differences between that ball and the bill as reported by the committee.]

DEPARTMENT OF AGRICULTURE,
Washington, D. C.

Hon. CHARLES W. WATERMAN,
Chairman Senate Patents Committee,
United States Senate.

MY DEAR SENATOR: Receipt of yours of the 21st instant, with inclosure of a copy of the bill S. 3530, introduced by Senator Townsend to amend section 4886 of the Revised Statutes, is acknowledged. As the result of examination of the bill by plant specialist of the department, the following comments and suggestions are submitted:

The evident purpose of the bill is to encourage the improvement of some kinds of cultivated plants, both through breeding and discovery of better varieties, by granting to the breeders or finders of new and distinct varieties of such plants the exclusive control over the reproduction of their creations and discoveries, presumably for the same period of years now covered by patents on inventions. This purpose is sought to be accomplished by bringing the reproduction of such newly bred or found plants under the patent laws which at the present time are understood to cover only inventions or discoveries in the field of inanimate nature. This it is proposed to accomplish by amending section 4886 of the Revised Statutes so as to make it possible to patent "any new and distinct variety of an asexually reproduced plant other than a tuber-propagated plant or a plant which reproduces itself without human aid." The operation of the present law is understood to rest upon the filing by the inventor of such properly authenticated verbal descriptions, designs, drawings, or other descriptive matter as will fully disclose the nature of his invention or discovery, thereby enabling one skilled in the art to which it relates to make effective practical application of the invention or discovery. Bill S. 3530 proposes in effect to authorize the patenting of certain distinguishable forms of plants which are capable of reproduction and multiplication through the operation of physiological processes with human aid.

Page 2, lines 8 to 13, which in the bill read as follows, "*Provided,* That the words 'invented' and 'discovered' as used in this section, in regard to asexually reproduced plants, shall be interpreted to include invention and discovery in the sense of finding a thing already existing and reproducing the same as well as in the sense of creating," interpreted in the light of agricultural and horticultural experience and history, would appear to make possible the patenting of the reproduction of any new and distinct variety wherever discovered, provided it meets the other specifications of the bill.

This possibility of reward would undoubtedly influence the public to be more observant of plants and thus tend to prevent the waste of many valuable new varieties which occur naturally but are now lost to mankind through neglect or lack of appreciation of their value.

***(*2 paragraphs omitted—included in preceding report on page* 357).

The proposed legislation would appear to be desirable and to lend far-reaching encouragement to agriculture and benefit to the general public.

Sincerely,
ARTHUR M. HYDE, *Secretary.*

Text of Bill

[The italics indicate the changes to be made in the existing patent laws.]

Be it enacted by the Senate and House of Representatives of the United States of America in Congress assembled, That sections 4884 and 4886 of the Revised Statutes, as amended (U. S. C., title 35, secs. 40 and 31), are amended to read as follows:

"SEC. 4884. Every patent shall contain a short title or description of the invention or discovery, correctly indicating its nature and design, and a grant to the patentee, his heirs or assigns, for the term of seventeen years, of the exclusive right to make, use, and vend the invention or discovery (*including in the case of a plant patent the exclusive right to asexually reproduce the plant*) throughout the United States and the Territories thereof, referring to the specification for the particulars thereof. A copy of the specification and drawing shall be annexed to the patent and be a part thereof.

"SEC. 4886. Any person who has invented or discovered any new and useful art, machine, manufacture, or composition of matter, or any new and useful improvements thereof, *or who has invented or discovered and asexually reproduced any distinct and new variety of plant other than a tuber-propagated plant*, not known or usde by others in this country, before his invention or discovery thereof, and not patented or discribed in any printed publication in this or any foreign country, before his invention or discovery thereof, or more than two years prior to his application, and not in public use or on sale in this country for more than two years prior to his application, unless the same is proved to have been abandoned, may, upon payment of the fees required by law, and other due proceeding had, obtain a patent therefor."

SEC. 2. Section 4888 of the revised Statutes, as amended (U. S. C., title 35, sec. 33), is amended by adding at the end thereof the following sentence: *"No plant patent shall be declared invalid on the ground of non-compliance with this section if the description is made as complete as is reasonably possible."*

SEC. 3. The first sentence of section 4892 of the revised Statutes, as emended (U. S. C., title 35, sec. 35), is amended to read as follows:

"SEC. 4892. The applicant shall make oath that he does verily believe himself to be the original and first inventor or discoverer of the art, machine, manufacture, composition, or improvement, *or of the variety of plant*, for which he solicits a patent; that he does not know and does not believe that the same was ever before known or used; and shall state of what country he is a citizen."

SEC. 4. *The President may by Executive order direct the Secretary of Agriculture* (1) *to furnish the Commissioner of Patents such available information of the Department of Agriculture, or* (2) *to conduct through the appropriate bureau or division of the department such research upon special problems, or* (3) *to detail to the Commissioner of Patents such officers and employees of the department, as the commissioner may request for the purposes of carrying this Act into effect.*

SEC. 5. *Notwithstanding the foregoing provisions of this Act, no variety of plant which has been introduced to the public prior to the approval of this Act shall be subject to patent.*

SEC. 6. If any provision of this Act is declared unconstitutional or the application thereof to any person or circumstance is held invalid, the validity of the remainder of the Act and the application thereof to other persons or circumstances shall not be affected thereby.

APPROVED MAY 23, 1930.

Applying the Plant Patent Law

The right to patent plants having been granted by Congress, the working out of the process of exercising this right by plant breeders or their assigns is likely to be a long and interesting story. The foregoing Committee Report will give breeders and botanists an inkling of the lack of knowledge in legal circles regarding the biological problems which will have to be met in the working out of the law. Botanists have been discussing for years the similarities and differences between mutants and sports, and it comes as something of a shock to learn that a mutant results "from seedling variation by self-pollenization of species." Granting that the botanist is able to form any conception of the meaning of the phrase "self-pollenization of species," he must be amazed to think that he and his fellows have been puzzled for so long by a process so simple! Reading further, he must have pondered long over the definition of a hybrid—which "results from seedlings of cross pollenization of two species, two varieties, or of *a species*

and a variety." The italics are ours, and they can be left as a symbol of the stupifaction with which botanists must have read many of the paragraphs of the Report dealing with their chosen domain.

On the legal side, plant specialists who contemplate obtaining plant patents have much to learn, as the report may have suggested. There is already in existence, ready to be applied to the patenting of plants an enormous body of legal decisions, and a complicated technique of rules promulgated by the Patent Commissioners. The rules with regard to the patenting of plants will doubtless be simplified as much as possible, but even at best, there will be complications at the start.

A recent statement regarding the new law, emanating from the office of a prominent patent attorney, which included among the methods of asexual reproduction that of *"hand pollenation,"* suggests the absurdities that may be expected!

Much reliance is placed in the report on the accuracy of botanical nomenclature as an aid to patent descriptions without realizing that much of this is quite inadequate to distinguish between varieties, where differences in flavor, odor, texture of flesh, and a multitude of other characteristics defy botanical differentiation. The Report fails to emphasize that much of the vocabulary of botanical nomenclature deals with characters of not the slightest economic importance, but having varying degrees of excellence for specific definition. Botanical terminology will be a great aid in defining new varieties, but it will not be enough. Other botanical devices, such as the standard color chart, of which Ridgeway's is at the present time the most widely used, will also facilitate definition of claims. In matters of color and flavor, and other characters having marked seasonal and regional variation, the practical importance of too microscopically accurate definitions is questionable. There is nothing to be gained by attempting to make imaginary distinctions of fluctuating characters.

The Type Plant

The Patent Office has ceased to require the submission of a model as a part of the patent application. It is difficult to see how a modification of the model, a type-plant, or type-orchard (or in the case of short-lived forms, some recognized standard) is to be avoided as an absolute necessity in the patenting of new plant varieties. The type plant will form practically the only accurate basis of comparison in the event of infringement suits. When the majority of pomologists frankly admit that they cannot begin to differentiate the existing varieties of fruits, the utter impossibility of relying on verbal descriptions, or even on drawings or photographs, begins to be evident. The type plant would remain the actual living embodyment of what was patented; it would eliminate the difficulty of defining the range of seasonal or regional variation of the variety, because by grafting on the type or by taking grafts from the type, the identity of any alleged infringement could be determined. This would take time, but it appears to be the only way in which to avoid endless confusion.

As the genetics of a larger number of plant species becomes more completely known, the relations of the genes and the chromosomes will doubtless be used in describing new varieties. This could be done under the existing statute. Maize is the only plant in which even provisional chromosome maps have yet been made, but in time others will follow, and the use of such descriptions in a patent will place the patenting of plants on a status very similar to that of the patenting of chemical compounds.

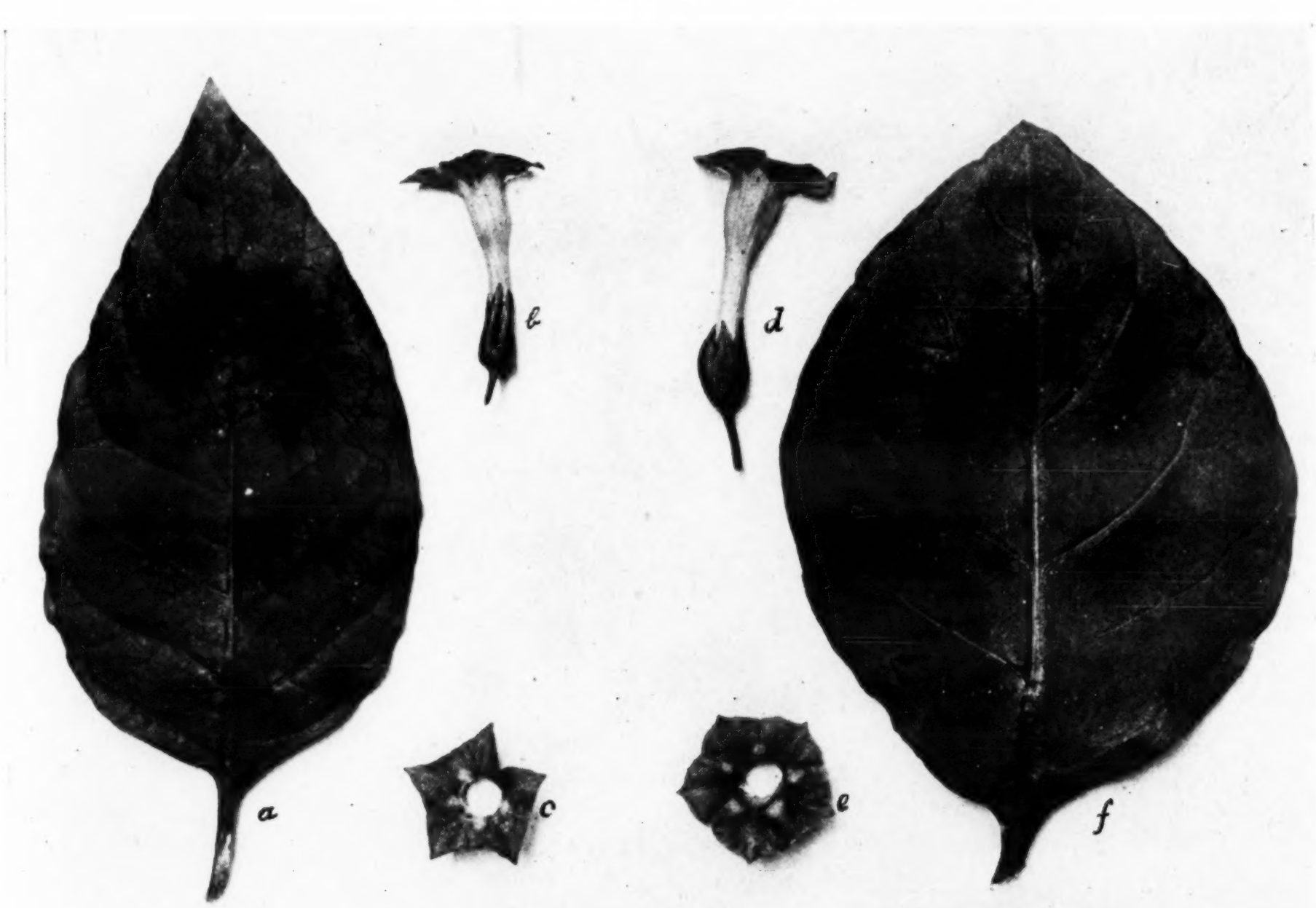
There will undoubtedly be many difficulties as yet entirely unrecognized to be overcome before the technique of granting plant patents and of protecting the patented varieties is satisfactorily worked out. Many details of

(*Continued on page* 369)

A PARTHENOGENETIC ABERRANT TOBACCO PLANT

JAMES KENDALL

Sofia University, Bulgaria



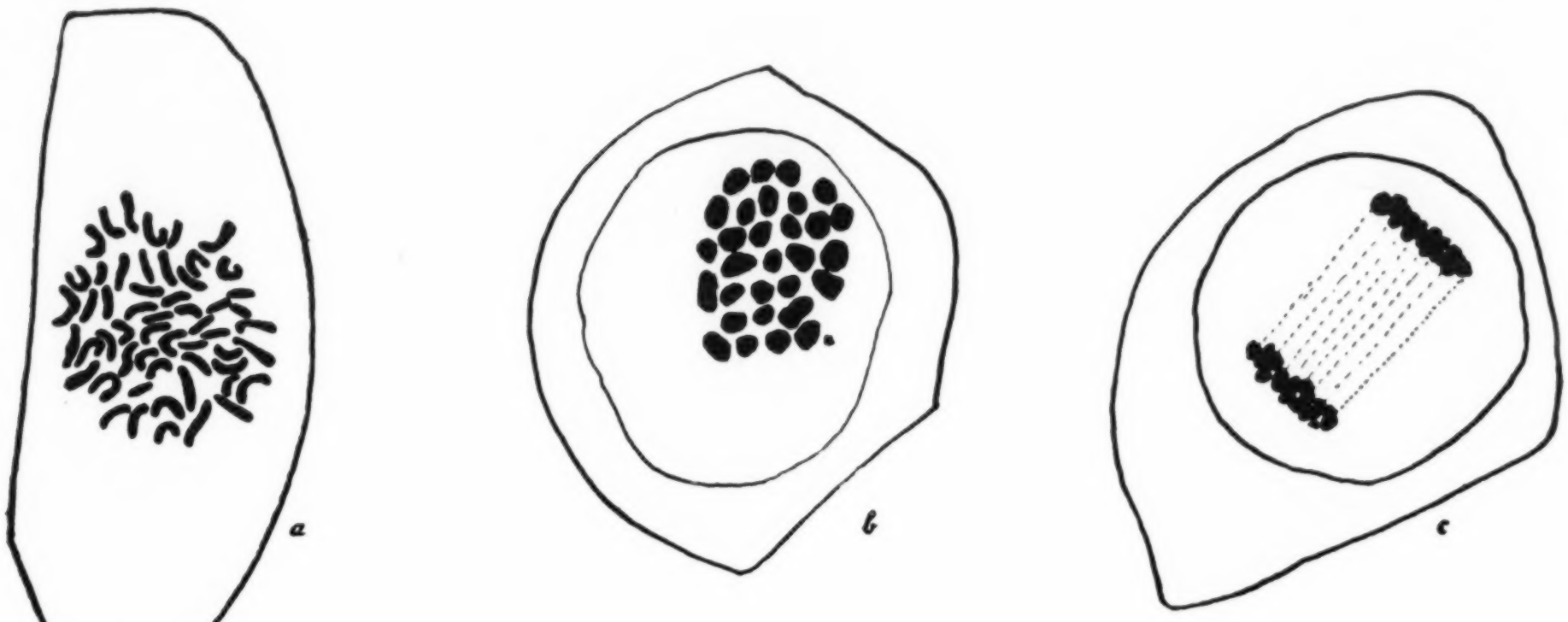
FLOWERS AND LEAVES OF ABERRANT TOBACCO PLANTS

Figure 4

Leaves and flowers characteristic of the parthenogenetic aberrant plant (a, b, and c) and those representing the type of the mother aberrant *Nicotian tabacum* plant (d, e, adn f). The parthenogenetic plant has 54 somatic chromosomes ; the moher plant has about 60 chromosomes. When pollinated with normal pollen about 50 per cent of the ovules produced viable seeds. Thus in crosses this plant offers possibilities of producing a great variety of new forms, some of which may prove to be stable.

IN a recent study of certain *Nicotiana* aberrants Kostoff (1930) reported the occurrence of aberrant plants in the progeny of a triploid *Nicotiana tabacum* that had been selfed. Among these aberrant plants with varying somatic chromosome numbers there were three with about 60 somatic chromosomes and 32 chromosomes in the pollen mother cells (PMC). One of these plants he pollinated with pollen from a blue pollen variety of *Petunia violacea* (n = 7) and observed that after such pollinations the ovaries became swollen. A study of the ovaries showed the majority of the ovules in such cases to be parthenocarpic, a few, however, were observed that contained small embryos. From ten capsules, about 600 seeds in all, obtained from flowers so pollinated a single plant was raised which will be described here.

This parthenogenetic plant differs



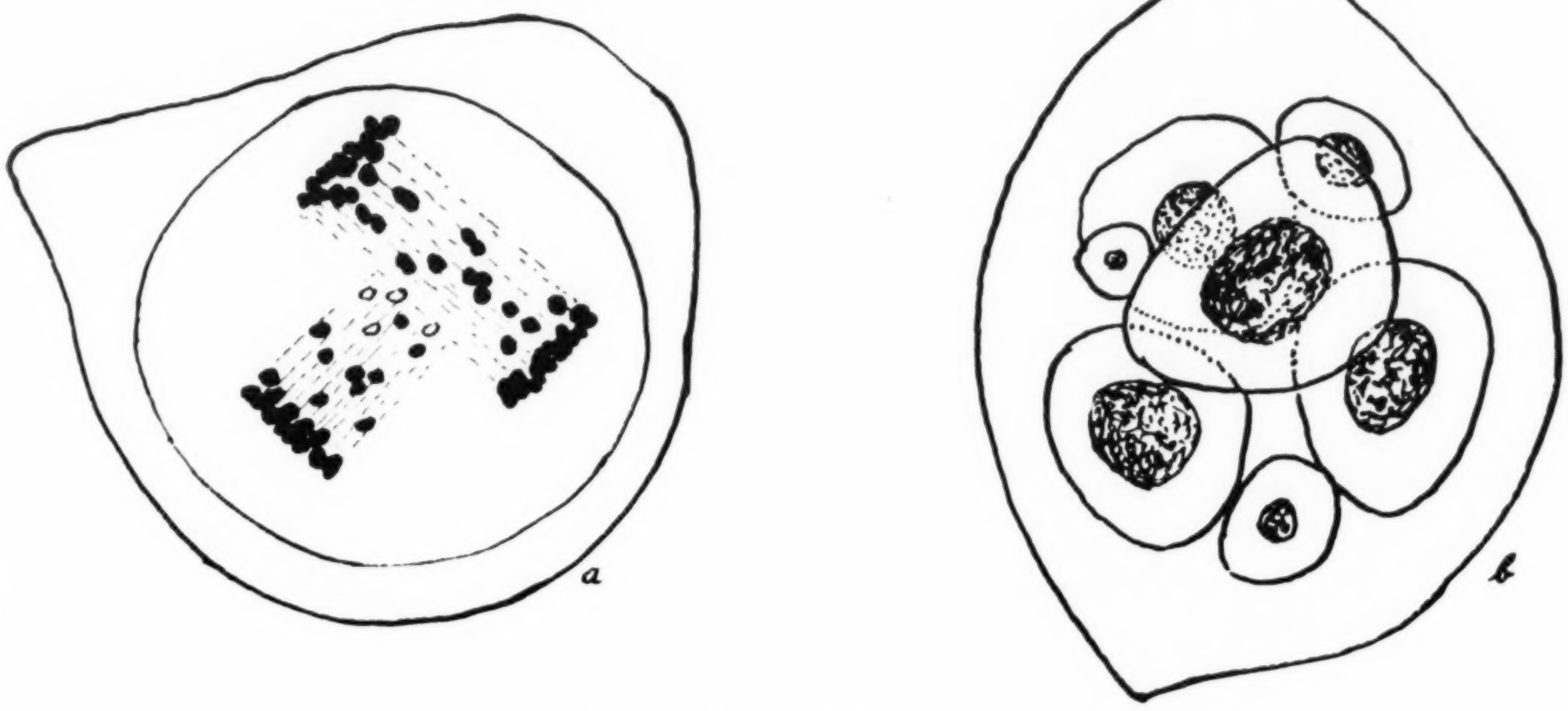
CHROMOSOMES OF THE PARTHENOGENETIC PLANT

Figure 5

(*a*) Somatic metaphase with 54 chromosomes. (*b*) Heterotypic metaphase of pollen mother cell with 30 chromosomes; (*c*) regular heterotypic anaphase from a pollen mother cell.

from the mother aberrant *Nicotiana tabacum* plant in its morphological characters, especially those of the leaf and flower. Features of the foliage and flower characteristics of the type of the mother plant are illustrated in the right half of Figure 4 (d, e, f) and those of the parthenogenetic plant in the left half of the same figure (Fig. 4 a, b, c). In the latter the foliage leaves are much narrower and taper in more than half their length toward the apex which in this instance forms an angle of about 45 degrees as compared to the much broader one of about 90 degrees of the leaf in Figure 4f. Furthermore, the leaves of the parthenogenetic plant have longer and more slender petioles. The flowers are smaller than those of the maternal type (fig. 4b and 4d); the petals are angulate and give a starlike form to the opened corolla (fig. 4c) as compared to those typical of the mother plant (fig. 4e) which are broader and rounded abruptly from the apex to give a wavy outline to the opened corolla. The calyx is also smaller than in the parent type, the sepals are narrower and less broadly fused together in the basal portions (fig. 4b and 4d).

The data obtained from a cytological study of the parthenogenetic aberrant are as follows. In the somatic metaphases in the cells of the root tips 54 chromosomes were counted (fig. 5a). A study of the floral buds during meiosis showed this process to be accompanied by irregularities, particularly marked in the second meiotic division. In the metaphases of the first meiotic division in the PMC 30 chromosomes were counted most frequently (fig. 5b), 29 and 31 were observed infrequently. Usually, this division was normal (fig. 5c), only rarely were instances observed where one or two chromosomes were leading the advance to the poles in the early anaphase or lagging on the spindle in the late anaphase. In the metaphases of the second meiotic division 26, 27, 28, 29, and 30 chromosomes were counted but most commonly the number was 27. Early anaphases of this division were sometimes observed with a few chromosomes leading the advance to the poles, while the late anaphases very often had a number of the chromosomes spread out along the spindle as illustrated in figure 6a. Due to the formation of nuclei from the groups of chromosomes still lagging on the spindles in the telophases of the second



IRREGULARITIES IN POLLEN FORMATION

Figure 6

(*a*) Irregular homœotypic anaphase in the pollen mother cell of the parthenogenetic plant. (*b*) A septad from the pollen formed by the parthenogenetic plant.

division pentads, hexads, and septads (fig. 6) were observed. Even in the cases where tetrads were formed the members were often of diverse sizes as a result of the unequal distributions of chromosomes in the second anaphase. The pollen contained about 75 per cent of abortive grains.

In order to explain the origin of this parthenogenetic aberrant plant it is necessary to recall the cytological conditions observed in the mother plant. There, meiosis was also observed to be irregular but the irregularities were most marked in the first division; the pollen was found to contain about 50 per cent of abortive grains and occasional dyads. It seems very probable that due to excessive lagging and distribution of chromosomes along the spindle this first meiotic division was not completed in the case of an embryo sac mother cell, as was observed to occur in the case of the PMC, and such a cell then proceeded to the second division without any reduction of the chromosome number, *i. e.*, it contained the diploid number of approximately 60 chromosomes observed in this aberrant plant. Then in the second meiotic division, where irregularities were observed in studying the PMC, the chromosomes have divided but due to non-disjunctions some of them have failed to separate and an unequal distribution occurred giving rise to one nucleus with 54 chromosome and another with 66, assuming 60 chromosomes originally present as observed in the case of the somatic cells. In the case of such an event there would be included in these 54 chromosomes one complete haploid set (24), one incomplete haploid set, and a few chromosomes from a third set of chromosomes contributed through non-disjunction. This would account for the irregularities observed in the second meiotic division of the parthenogentic plant where the metaphases with 26, 27, 28, 29, and 30 chromosomes would often represent two incomplete sets of chromosomes. Such conditions would further increase the percentage of abortive pollen grains, for not only are those with less than the haploid number of chromosomes unviable but also those having more than the haploid number (as

those with 26-30 which may represent sums of incomplete sets) but still not having a complete haploid set. This appears to be the most reasonable interpretation of the origin and constitution of the parthenogenetic aberrant plant. Other instances of parthenogenetic plants have been observed in *Nicotiana,* the majority of them are of the diploid type such as that reported here (Thomas[5], Wellington[6], Kostoff[3], etc.), only a few are of the haploid type (Clausen and Mann[1], Ruttle[4]).

This parthenogenetic plant formed very few seeds when selfed but when crossed with normal *Nicotiana tabacum* about 50 per cent of the ovules developed normal seeds. The egg cell, though in many cases also presumably without a complete haploid set of chromosomes, though containing more than the haploid number of *Tabacum,* is evidently not subjected to such a trial of viability as the pollen before receiving from the male gametes a complete set. This is shown by the appearance of the higher percentage of viable cells, judging from the ovules developing after pollinating with the original form, than are found in the pollen. This plant with its characters and chromosome number differing from those of the original form offers a source for the production of a multiplicity of new forms some of which may stabilize. Plants are now being raised from the seed obtained from the cross with the normal *Nicotiana tabacum* mentioned above.

The author is indebted to Dr. Kostoff for the material for the present paper.

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(*Continued from page* 356)

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A NEW EUGENICS BEQUEST

British Eugenics Society Receives Half-Million Dollar Legacy

BY the will of Mr. Henry Twitchin, who died in France on March nineteenth, the British Eugenics Society is to receive the residue of his estate, totaling some £100,000, or roughly, $500,000. Mr. Twitchen had been an anonymous contributor to the society for a number of years. The income from this bequest will make available some $15,000 annually to be used by the Council of the society as it shall see fit. It was the implied wish of the testator that the income be used for eugenic propaganda rather than for research.

There are some very interesting parallels and contrasts between the Twitchell bequest and the Metcalf bequest to the American Genetic Association,* which will ultimately yield an income of nearly $5,000 per annum, to be used in much the same way but with emphasis on research rather than on propaganda.

It is perhaps significant that both men started life as immigrants to a new country and that both made their fortunes in live stock. Twitchin's interest in heredity was strengthened by the belief that he himself was the victim of hereditary weaknesses, and in a letter to Major Leonard Darwin in 1922, he traces the history of his interest in the subject:

> I first became interested in Eugenics about 25 years ago, when the idea of applying the principle we had for a long time made use of in improving our farm stock to the improvement of the human family occurred to me just as originally as it did to the Founder of our Society, to the Greeks of old, and no doubt to many others. This is not to be wondered at when it is known that I am descended from a long line of countrymen at home, some of whom helped to make our domestic animals what they are today, that I was live stock prizeman at the Downton Farming School in 1888, and since then have devoted my whole life to the breeding of live stock (over 40,000 last year), in which, as you know, under the best practice, the principle of eugenics is the controlling factor.
>
> Although my occupation alone would naturally have led me to this conclusion, it was the fact that I was born of unsound parents and inherited their weaknesses and consequently have suffered thereby, that first forced this question upon me. Isolated as I was in what was then the Back Country here, I had no opportunity of discussing it with people who were likely to know what had already been done to make the idea of use to the world, although it was certainly explained to one or two of my more enlightened neighbours, and it was years afterwards that I met with a reference in some paper (The *Times Weekly* probably) to the work of the late Henry [Francis] Galton, and of the founding of the Eugenics Education Society.
>
> Applying the great principle, as I was constantly doing in my work, it was natural perhaps for me to see no difficulty in doing the same at once with men and women. And I was then advocating the immediate introduction of legislation in all civilized countries prohibiting the propagation of the unfit from any cause. But after reading some of the publications by the Society and other works on the subject, I realized that the great majority of the people were not ready for such a revolutionary change, and that the best course to bring about the desired improvement was to do as the Society was doing and educate, if possible, the masses to see the inestimable advantage of adopting the principle and gradually enforce control. . . . .
>
> Believing in practice as well as in principle, I never married, although better fitted to do so probably than fully one-half of those who do—and being the last of my family I have no relatives having any claim on my property I, in 1912, made my Will—after providing for certain legacies—in favour of our Society, for the carrying on of the propaganda which I believe to be by far the most urgent and important work possible in human endeavour. . . . . .

Like Metcalf, he guarded himself against being considered foolish or hasty in the disposal of his property for so "impractical" a purpose, by a detailed statement of his views. This was not a part of the Twitchin will but was

*For a text of the Metcalf will see *Journal of Heredity* 19:97-103, 1928. A copy of the text of the will may be obtained by members by applying to the office of the Association.

contained in a letter to the Public Trustee and was filed with one of the earlier wills.

Lest it should be considered that in bequeathing the whole of the residue of my estate, as I have done, for the purposes of furthering the knowledge and, I trust, in time securing the adoption of the principles of eugenics both in England and throughout the world, I have acted hastily. . . . . I am desirous of mentioning by letter to you that . . . . . I have for nearly 20 years past taken the keenest interest in all aspects of eugenics and have read and thought much upon the subject and, in the result, I am thoroughly convinced that to the extent the knowledge of the science is brought home to the people and its principles acted on and enforced, enormous beneficial results must inevitably follow, and it is to aid and assist in this that I very thankfully devote the bulk of my property.

In the *Eugenics Review* for July, 1930, Major Darwin gives a detailed statement of Mr. Twitchin's relations with the society. In reply to the preceding letter Major Darwin set forth the aims of the Society as follows:

As to the methods of utilizing any further funds coming under the influence or control of our Society, that is a point on which I could say a great deal, and is one on which you will probably wish to hear something. We now often miss an opportunity of getting a lecture delivered on eugenics because we cannot afford to give any remuneration to our lecturers. If we could pay even a moderate fee, we should soon get together a capable band of lecturers, and, being able to comply with any demand, the work in this direction would soon be largely increased. Our REVIEW, as a method of propaganda, would be improved if we could afford to pay something to our contributors. Research in certain directions is at a standstill for want of funds. I have in my mind especially certain half-finished work in connection with the pedigrees of London pauper stock, which would be valuable from a scientific point of view, and most helpful to lecturers to illustrate existing evils due to heredity. Lastly, our staff is ill-paid and inadequate which makes all progress difficult. This is perhaps sufficient to show how greatly the whole position might be strengthened were more funds available. There is no institution throughout the world known to me which is carrying on such an active eugenic propaganda as we should desire to initiate had we the means; and for any Society to set a proper example in this respect might produce beneficial results to posterity of incalculable magnitude.

Many interesting excerpts from Mr. Twitchin's correspondence are given in this article, but space permits only the two following:

Perhaps no one but those who have had the management of large stock farms fully realize the practical side of this question. We know the utter madness of going on breeding up when the Ranch is fully stocked and there is no, or insufficient, outlet for the surplus. . . . If it is to do any good we must banish sentiment and act drastically. We must not consider the rights of individuals over-much—a lunatic in my opinion has no rights—when the vital interests of the State are at stake.

I should not, if I were you, condemn "stockyard methods," so called, so severely. What are they but the practice of the very essence of eugenic principles—the prevention of the breeding of the unfit and making it possible for only the best types to do so. It may be good policy for the present not to go too far, but if eugenic teaching is ever to do any practical good for the human family, stronger measures will have to be taken than any so far advocated. The other book you sent me, "Posterity," is, I think, a most useful contribution to the subject, very clearly and concisely stated and going a little further than you do in suggesting immediate remedies . . . . . The late Health Minister could only propose keeping mental deficients (300,000) in colonies and after some training letting them out under supervision as though they could then be prevented from propagating. Could anything be more childish? . . . Progress is slow, but the only way is to keep pegging away like a patient fisherman hoping for a bite sooner or later. I think we must look for the greatest developments in the newer countries, like America, where deep-rooted prejudice is not so strong as it is in our country; and yet it is here that eugenic reform is most needed to get rid of the great burden of the unemployed.

The legal status of the funds bequeathed to the Eugenic Society by Mr. Twitchin, differs quite markedly from that of the Metcalf fund, which was left in trust with the Council of the American Genetic Association, the income to be spent in any way that Council may direct. The Twitchin estate goes to the Eugenic Society without any such limitations, although with an expressed hope that the interest alone would be expended:

It is my desire that the aforesaid bequest should constitute a permanent fund and that

the income derived therefrom should be used for furthering the objects of the Society, including the support of branches of the Society, but I expressly direct that such desire shall not impose legal obligation on the Society or prevent the expenditure of capital if such expenditure is deemed expedient at the time.

This represents a middle course between a trusteeship and the tendency in some quarters to require the expenditure of both principal and interest in a given number of years. Either of these arrangements lack elasticity and tie the hands of those who have the administration of such funds, and whose decisions under changing conditions and in emergencies would on the average be wiser than any action, or lack of action, necessitated by being forced to handle such bequests in a purely static manner.

It is a curious and striking fact that the only two bequests made for race betterment since that of Galton have been made by stockmen. Perhaps it is only a coincidence, but probably it has a deeper basis—both men realize the futility of trying to ameliorate the conditions of living without taking thought as to the quality of the people who are to benefit by such bequests. It is coming to be recognized more and more that philanthropy that does not take thought of its by-product results, may ultimately do more harm than good. "The kind of people we are determines our destiny," and philanthropic bequests are having an increasingly important effect in determining this vital matter. Metcalf and Twitchin realize that the groundwork of knowledge of facts about heredity has not yet been prepared, and without this the permanent value of what may be classed as "ameliorative bequests" may well be questioned.

Perhaps up to the present, men who deal with heredity every day are the only ones able to realize the importance of further study and to understand the need to make available what is already known. Thus these two wills are in the nature of a challenge to others who are able to make bequests to benefit their fellow men. The statement that heredity is basically important deserves careful consideration. If it is true, an obligation rests on those able to give, to see that adequate funds are available for research and for dissemination of knowledge regarding human heredity. If it is true, there is serious risk of doing more ultimate harm than ultimate good in bequests for the betterment of social conditions. Metcalf and Twitchin realized this clearly, but must the advancement of this view, so important to the welfare of the race depend entirely on those who combine business acumen and sheep-raising ability, or are there others in other fields of endeavor who are advanced enough to stand with these two men as pioneer benefactors in the vital field of race betterment?

Applying the Plant Patent Law

(*Continued from page 362*)

patent office practice will have to be modified, because much more than with machines and physical phenomena generally each species of plant is something of a law unto itself. None of the obstacles should prove insurmountable, and now a beginning has been made they will eventually be surmounted,—even the greatest difficulty of all, the by no means remote possibility that the Supreme Court may declare the present statute invalid as exceeding the power granted to Congress by the Constitution. After the law in its present form, or as modified, has begun to function smoothly, justice demands that it be extended to cover sexually reproduced varieties. In the last analysis, this is the field most needing patent protection for no sexually reproduced variety can possibly be the result of casual hybridization, or a chance find, as are many varieties in the field covered by the present law.

They are all the product of deliberate planning and persistent effort necessarily extending over many years, and thus especially deserve protection.

There appears to be a serious difficulty in such an extension of the statute in the fact that in many such crops the seeds are the part of the plant which is used commercially. In such crops as cotton and flax the seeds, or seed products, are important as articles of commerce, but very little of the seed itself reaches the ultimate consumer, and the difficulties of protecting seed supplies do not seem insurmountable. The distinction between commercial and agricultural uses of the seeds certainly is not as serious nor as difficult to maintain as the distinction between industrial and beverage alcohol. In one respect seeds have a great advantage that once they are denatured by killing the embryos no process at present known or likely to be discovered can make the seed again suitable for the "bootleg seed trade!"

The distinction made by the committee on this point is really entirely artificial, because in the nursery trade the thing sold is the plant itself, which is just as capable of reproduction as any potato bought at a chain grocery store. In the florist trade every rose and gardinia which moves across the counter, while not ideal propagating material, is nevertheless potentially capable of being reproduced by budding or rooting. Thus while the inclusion of sexually reproduced plants might add to the complexity, it would raise few new issues, and will ultimately be demanded, because all of our major crops except the tuber-reproduced crops are to be found in this category. Much of the enthusiasm for the law in its present form as an aid to agriculture is thus seen to be somewhat unjustified. Until the breeders of new varieties of such important crops as the grains and cotton and tobacco share in the advantages conferred by patent protection, plant patent legislation can hardly be considered to have reached its final form.

Patent Office Rules Regarding Plant Patents

It is understood that a number of applications for plant patents have been received by the Patent Office, and that others are being prepared by patent attorneys in Washington. Little official information is available. A recent statement to inquirers by the Chief Clerk of the Patent Office gives the present status of the rules governing plant patents:

> The rules of practice governing the filing of applications for patent under the plant patent act (Public No. 245) approved by the President on May 23, 1930, have not been completed, but applications will be accepted for any plant which is believed to be patentable under the new law. The fees will be the same as for mechanical patents.[*]
>
> In filing an application the specification should be in duplicate and the drawing also, where colors are involved. Color drawings must be made on heavy Whatman paper in permanent water colors. Where color is not a variation upon which the plant depends for its patentability the drawing may be filed in black and white, in which case only one copy of the drawing will be necessary. The reason for filing the drawings and specifications in duplicate is that it may be necessary to have the experts in the Agricultural Department pass upon the applications as to whether or not the variety is new, and in such cases the Office would not care to allow the original application to pass out of its possession.
>
> As soon as the new rules are formulated they will be published in the Official Gazette of the Patent Office which may be found in most large public libraries.
>
> It should be noted that Section 5 of the act of May 23, 1930, provides that no variety of plant which has been introduced to the public prior to the approval of the act shall be subject to patent.

*The fees are $25.00 payable upon filing of the application for patent, and $25.00 additional upon final issuance of the patent. This does not, of course, include fees of a patent attorney employed for the preparation of the technical specifications and claims, and the prosecution of the case before the Patent Office. The employment of an attorney is not mandatory, but as the value of a patent depends largely on the drawing of the claims the qualifications of an attorney are important.—*Editor.*

A STUDY OF LIKE-SEXED TWINS

III—Twinning Among Relatives

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TWINNING in man presents three interesting problems for the geneticist: (1) Is it an hereditary trait? (2) If it is, are the methods of inheritance the same for both monozygotic and dizygotic twinning? (3) Does heredity act equally through the mother and father? Dahlberg,[1] in summarizing the literature and some of his own data, comes to the following conclusions: "Heredity of the disposition to bear dizygotic twins, has been shown to exist in the mothers. Hereditary dispositions of the father of dizygotic twins, are probably of no importance. For monozygotic twins, also, heredity probably exists, and the disposition probably can be present both in the father and the mother."

It may be noted that, in spite of these conclusions, Dahlberg's own results are not very fully in support of the inheritance theory. Davenport[4], working with a fairly complete body of material, had previously concluded that twinning of both types "depends on constitutional-hereditary-factors on both sides of the house."

Like most problems concerning human heredity, study has been handicapped by the scarcity of adequate material. The most valuable data would consist of genealogies for a large number of twin bearing families and similar data for a "control" group of normal families. Such records are, of course, difficult to secure.

In the course of a study of some two hundred twins at the Institute of Child Welfare, considerable data were secured concerning other cases of twinning among the relatives of our sample children. As some of this information seems pertinent to the general study of the inheritance of twinning in man, it will be summarized and briefly discussed in this paper.

Our sample consists of like-sexed twins of school and pre-school age. Their parents are predominately native white, and of North European descent. A full description of the sample and discussion of the method of securing the data are given in a previous paper.[2]

Through interviews made with the mothers all possible information was secured concerning other cases of twinning among relatives of the twins of the sample. No doubt the data are incomplete with regard to pairs or individuals who died at birth or in early infancy; they should, however, include the great majority of other cases occurring in the nearer branches of the family.

All of the information obtained is summarized in Table I. As the pairs have been segregated into groups of identical, fraternal, and "undetermined" types the data for each group are given separately. The number of pairs in each of these groups is included in Table II. The number of "undetermined" is too small to warrant much discussion here; further study will probably distribute these pairs about equally between the other two groups.

The data secured are of three different kinds which may be divided as follows:

1. *The percentage of twins among the siblings of the pairs of the sample.* Record was made of all the siblings of the twins studied and in some cases there were more than one pair of twins in the family. The number of these cases is small, but the data do give some measure of the tendency

of twinning mothers to "repeat themselves."

2. *The percentage of twins among the near ancestors of the pairs of the sample.* When the data for the parents and grandparents are segregated we have a measure of the twinning tendency in these close progenitors which may be compared with the population at large. Incidentally, the information received concerning cases of twinning in these groups should be quite accurate.

3. *The number of twins reported among all the relatives of the pairs of the sample.* The *percentage* of twins in this group can not be ascertained because the total number of

TABLE I Twin Pairs Among Relatives of the Twins of the Sample

Relation to twins of the Sample	Twin Relatives of 88 Prs. of Identical twins					Twin Relatives of 92 Prs. of Fraternal twins					Twin Relatives of 18 Prs. of undetermined twins					Grand Total
	♀♀	♀♂	♂♂	Sex Unknown	Total	♀♀	♀♂	♂♂	Sex Unknown	Total	♀♀	♀♂	♂♂	Sex Unknown	Total	
Siblings	0	0	0	0	0	0	4	0	0	4	1	0	0	0	1	5
Twins on maternal side in Direct line																
Mother - one of twins	2	1	0	0	3	0	0	0	0	0	1	0	0	0	1	4
Grandmother-one of twins	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Grandfather - one of twins	0	0	2	0	2	0	1	1	1	3	0	0	0	0	0	5
Twins on Paternal side direct line																
Father - one of twins	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	2
Grandmother - one of twins	2	0	0	2	4	1	0	0	1	2	0	0	0	0	0	6
Grandfather - one of twins	0	0	0	1	1	0	0	0	2	2	0	0	0	0	0	3
Prs. on maternal side not in direct line																
Twin siblings of mother	4	1	1	3	9	4	1	6	5	16	1	1	0	1	3	28
Twin siblings of Grandmother	1	0	3	0	4	0	1	3	0	4	0	0	0	0	0	8
Twin siblings of Grandfather	0	0	0	0	0	0	1	2	1	4	0	0	0	0	0	4
Twin offspring mother's sister	0	1	4	3	8	2	1	2	1	6	0	1	0	0	1	15
Twin offspring mother's brother	0	0	0	1	1	3	1	1	0	5	0	0	0	0	0	6
Prs. on Paternal side not in direct line																
Twin siblings of father	3	1	4	1	9	2	1	2	4	9	0	1	0	0	1	19
Twin siblings of Grandmother	1	0	0	0	1	0	0	0	4	4	0	0	0	0	0	5
Twin siblings of Grandfather	1	0	1	1	3	0	0	0	0	0	0	0	0	0	0	3
Twin offspring Father's sister	2	5	1	0	8	2	2	0	2	6	0	1	0	0	1	15
Twin offspring Father's brother	0	0	2	3	5	3	0	1	0	4	0	0	0	0	0	9
Twins among more distant relatives																
Maternal	11	7	8	27	53	9	8	8	20	45	1	0	2	12	15	113
Paternal	4	2	3	16	25	2	2	2	12	18	1	0	1	4	6	49
Totals	31	19	30	58	138	28	23	28	54	133	5	4	3	17	29	300

TABLE II Cases of Twinning Among Parents and Grandparents of Twins.

Group	Sample	Twinning Among Parents				Twinning Among Grandparents				Twinning Among Parents & Grandparents Combined						
										Maternal		Paternal		Combined		
	Number of Pairs.	Number of Parents	Mothers who were members of twin Pairs	Fathers Who were members of twin Pairs	Total Cases Among Parents	Total Number of Grand-parents	Maternal Grand-parents Who were members of twin Pairs	Paternal Grand-parents Who were members of twin Pairs	Total Grand-parents Who were members of twin pairs	Total Number of Parents & Grand-parents	No. of Parents & Grand-parents Who were Members of twin pairs.	Total Number of Parents & Grand-parents	No of Parents & Grand-parents Who were members of twin pairs.	Total Number of Parents & Grand-parents	No. of Parents & Grand-parents Who were members of twin pairs.	Percent of Parents & Grand-parents Who were members of twin pairs.
Identical	88	176	3	1	4	352	3	5	8	264	6	264	6	528	12	2.3±.6
Fraternal	92	184	0	1	1	368	3	4	7	276	3	276	5	552	.8	1.5±.5
un-determined.	18	36	1	0	1	72	0	0	0	54	1	54	0	108	1	.9±.7
Total	198	396	4	2	6	792	6	9	15	594	10	594	11	1188	21	1.8±.3

relatives is not known. However, the data for the identical and fraternal groups should be comparable. The data relative to maternal and paternal lines should be indicative of tendencies although they are more subject to systematic error (this will be discussed later).

In considering our data it must be born in mind that our group, consisting of like-sexed twins only, contained a higher proportion of monozygotic pairs than would a group containing the normal number of unlike-sexed pairs (about one-half of our twins were identical while in the general population about one-third are identical). For this reason, the relatives are also "selected" because they represent only the relatives of like-sexed twins.

Twin Bearing Mothers

If there is in certain couples a tendency to bear twins, we would expect this tendency to be in effect throughout their productive period. There would be a greater chance that some of their other children would also be twins than that the children of parents without this tendency would be twins (allowances being made for age of parents, family size, etc.). Of course, should such a tendency be found other data would be necessary to prove it an inherited trait.

The records for California for the years 1919-1924 show that 2.12 per cent of the children born were twins.[3] The twins of our sample had had 390 siblings (some were dead) among whom were 5 pairs of twins, (Table I). In other words, about 2.1% of children born in the general population were twins while among the siblings of the twins of our sample the rate was 2.7 ± .6. The data are too meager to have anything but negative significance, but there is no indication that mothers of one pair of twins have a much greater tendency to have plural births among their other children than do the mothers of the general population.

Twins Among Near Ancestors

When we segregate the data for the parents and grandparents (Table II), we find that only 1.8 ± .3% of these individuals were themselves members of twin pairs. The data are again too meager to be conclusive but apparently there were no more twins among the parents and grandparents of the twins of the sample than there are in the population at large*. This, of course, does not preclude the possibility that twinning is an hereditary trait. We know that the death rate of twins is very high and therefore relatively few of them live to have children[1]—if we should take any sample of children, either twins or single born, we would find that few of their parents or grandparents were twins. However, there still might be strong twinning tendencies present; this would be proven if it were found that these near ancestors had had a high percentage of twin siblings, although they themselves might never have produced twins. Unfortunately, we can make no estimate of the rate of twinning among these other rela-

*In the school population from which our sample was drawn, we found that 1.40% of the children were twins.

TABLE III: CASES OF TWINNING AMONG OTHER RELATIVES OF TWINS

		Number with record of twins among relatives on either or both sides of family	Number with record on maternal side only	Number with record on paternal side only	Number with record on both maternal and paternal sides
IDENTICAL	88	68	25	20	23
FRATERNAL	92	68	31	18	19
UNDETERMINED	18	12	5	3	4
TOTAL	198	148	61	41	46

tives because data on the single born are not available.

Jordan[5] gives the pedigrees of two twinning families. In these two genealogies 314 single born are recorded of whom 21% married and had offspring, 5.5 being the average number of children per family. Of the 42 twin individuals only 7% (3 individuals) had children; the average number of children per family being 4.3. This is quite striking evidence for the relatively low fecundity of twin born individuals.

When the data for the identicals and fraternals are compared it is found that of the four cases in which there were two or more pairs of twins in a family, none occurred in the identical group, 1 occurred in the "undetermined" group, and 3 occurred in the fraternal group. This, of course, could be entirely due to chance.

The identicals had a higher percentage of twins among their parents and grandparents than did the fraternals. However, the difference is not statistically proven. When we compare the records of the two groups for all the pairs of any degree of relationship (Table I), we find that the numbers are almost the same for both (138-133).

Maternal vs. Paternal Influence

Among the 1188 individual parents and grandparents there were 10 twins on the maternal and 11 on the paternal side. Of the total 300 twin pairs reported among all relatives, 187 or 62% were on the maternal side. This may be due to the fact that the mothers, from whom the data were secured, were able to give more complete data for their relatives than they could for the relatives of their husbands.

There were 148 cases in which other twins were recorded among relatives (Table III); in 41 or 27% of these the record was on the *paternal side only* and these cases were about equally distributed between the identical and fraternal groups. This appears to be in disagreement with Dahlberg's contention that there is no male transmission of the tendency to produce dizygotic twins. Of course, in these cases in which all twins among relatives are on the paternal side, there remains some possibility of a latent twinning tendency on the maternal side. Our data, however, align better with Davenport's[4] theory than with that of Dahlberg.

Summary

Through interviews with the mothers of 198 pairs of like-sexed twins data were secured concerning all other cases of twinning known to have occurred among the relatives. It was found that:

1. There was little indication that women who had had one plural birth tended to repeat the phenomenon.
2. Among the parents and grandparents of our sample, twins were no more common than in the general population.
3. There was little reliable difference between identical and fraternal groups in the comparisons made.
4. The data showed no reliable differences between maternal and paternal influence.

The data are too meager to disprove the inheritance of either monozygotic or dizygotic twinning, but they do seem to indicate that if the tendency is inherited it must depend for its survival upon transmission through the single born rather than through the germ plasm of the twins themselves.

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GENETICS OF COTTON

A Survey of Our Present Knowledge

THOMAS H. KEARNEY

(Continued from page 336)

Petal Spot

A DARK red or purple spot or "eye near the base of the petal characterizes many members of the genus Gossypium. The spot is entirely absent in most Upland cottons but is normally present, in varying degrees of size and intensity, in cottons of the South American group (Sea Island, Egyptian, etc.) and in many of the Asiatic cottons.

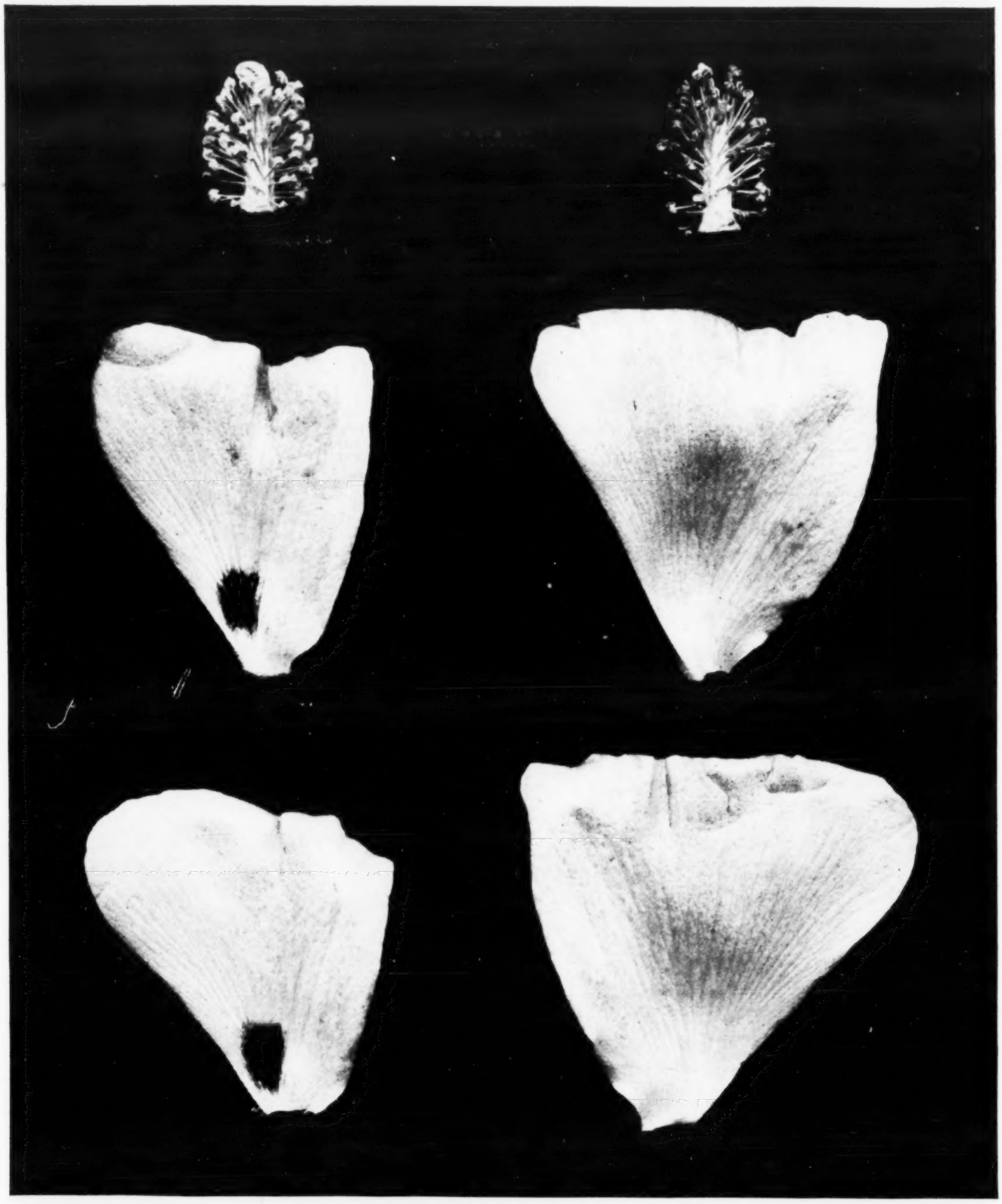
In a cross between a spotless and a strongly spotted Asiatic cotton, Leake and Prasad[37] found complete dominance of the spot in F_1 and 3:1 segregation in F_2. Kearney[28] crossed two forms of the Pima variety of Egyptian cotton, one having the spot absent or very weakly developed, the other having the large, intensely colored spot normal to the variety. Full spot was almost completely dominant in F_1 and a clear-cut segregation into 3 spotted, 1 "spotless" was obtained in F_2. Owing to the nearly complete dominance of full spot the homozygous spotted and the heterozygous F_2 plants could not always be distinguished but progeny tests proved that the spot tends to be less strongly developed in the heterozygotes than in the homozygous dominants. There were grown 24 F_3 progenies, 8 of spotless or very weakly spotted F_2 plants, 8 of spotted F_2s which showed the maximum development of the spot and 8 of spotted F_2's which showed the minimum development in this class. All F_2 individuals of the first two classes bred true, while all F_2 individuals of the third class gave segregating progenies, the ratio in no case departing significantly from 3 spotted: 1 "spotless."

Carver[8] in an Upland×Upland cross between a form (Red Leaf) having spotted petals and an entirely spotless form, obtained in F_2 close approximations to ratios of 3 spotted: 1 spotless. Two families, homozygous, respectively, for intensely spotted and spotless petals, have been isolated by Kearney from a mixed stock of the King variety of Upland cotton. (Figure 7.) The inheritance, in crosses between them (data unpublished) was similar to that described by Carver.

In a cross between normally spotted Sea Island and the "spotless" family of Pima, both presumably representing the same species, *Gossypium barbadense*. Kearney (data hitherto unpublished) obtained clear-cut 3:1 segregation in F_2, the minimum of the spotted class and the maximum of the "spotless" class having been separated by three full grades. These results of Leake and Prasad, of Kearney and of Carver justify the conclusion that in crosses within the same species, spotless or very weakly spotted petal behaves as a simple recessive to full-spotted petal.

Results obtained with interspecies hybrids also indicate that one main pair of allelomorphs is involved but that the action of different modifying factors derived from the different parental species results in segregation being less clear cut than in intra-species crosses, the F_2 distribution showing usually no distinct gap between the spotted and spotless classes. The data published by Balls[4,5] and Kearney[27] on Upland-Egyptian hybrids, by McLendon[38] and Kulkarni and Khadilker[34] on Upland-Sea Island hybrids and by Harland[11] on a hybrid between Sea Island and "St. Croix Native" all admit of this interpretation.

Harland[19] reviews previous investigations and presents the results of his own numerous crosses among Ameri-



PETAL SPOT AND POLLEN COLOR

Figure 7

Petals and stamens of two families isolated from a mixed stock of the King variety of Upland cotton, one (left) homozygous for intensely spotted petals and cream-colered pollen, the other (right) homozygous for spotless petals and yellow pollen. In crosses between the two families, F_1 showed incomplete dominance of spotted petals and of yellow pollen and F_2 segregated for both characters in approximately 3:1 ratios. Natural size. Photograph by H. F. Loomis.

can cottons. He states (p. 368): "It is clear that there is no definite line of demarcation between spot and spotless, and the lowest grade of spot must consist of a single pigmented cell." He distinguishes 22 grades of spot (Plate IX, colored) in the various types with which he worked, but even less red color than in his very minute grade 1 was observed in some flowers. "New World cottons comprise all grades of spot, from a large purple blotch which occupies the whole claw of the petal to a single pigmented cell, the latter being frequently extinguished by fluctuation. Thus, . . . we are in ignorance whether

'spotless' really exists at all, or whether in all cases we are merely dealing with more spot or less spot." (p. 368). In crosses of "Cassava" (an apparently spotless form of *G. purpurascens*) with spotless Upland, traces of spot appeared in 23 per cent of the F_2 plants, one plant grading as high as No. 11 of Harland's scale. A spot gene possessed by but not phenotypically expressed in the Cassava parent, combining with modifiers derived from the Upland parent, is thought to be the explanation (p. 371). In the cross spotless Upland × Sea Island White Flower, the latter a weak-spotted form, 23 per cent of the F_2 population showed a higher development of spot than was observed in the Sea Island parent. (pp. 376-8). "Cassava," crossed with full-spotted Pima Egyptian, was the only one of Harland's crosses showing clear-cut monohybrid (3:1) segregation (p. 372).

Harland considers his results to have demonstrated the existence of a series of allelomorphs for petal spot and that "modifying factors may profoundly affect the development of spot in a plus or minus direction. . . . The rule that the difference between a dominant and a recessive may be reduced, almost if not quite, to the vanishing point by modifying factors has been found to hold good not only for spot on the petal, but also for the characters Pollen colour, Corolla colour and Red leaf."[19] (pp. 382, 383). The great amount of fluctuating variation shown by this character makes classification of the populations often a matter of difficulty. Quantitative evidence on this point is given by Kearney[28] (pp. 504-508).

Pollen Color

Upland cottons commonly have very pale-colored pollen, the shade usually designated as "cream," while in cottons of the Peruvian or South American Tree group the prevailing color is bright or deep yellow.

Data on inheritance of this character in intra-species crosses appear to have been published only by Harland and by Carver. Harland[20], (p. 391) crossing two cottons of the Peruvian type, one of which had deep yellow pollen (grade 3) and the other "white" pollen (grade 0) found yellow almost completely dominant and a clear-cut 3:1 segregation in F_2. In a cross between two Upland cottons which had, respectively, cream-colored (grade 0 and pale yellow (grade 1.5) pollen, he reports similar results. Carver[8] crossed an Upland having "white" pollen with an Upland having "buff" pollen and reports dominance of "buff," with 3:1 segregation in F_2 and confirmatory evidence from back crosses as to the mono-hybrid nature of the character.

Similar behavior has been noted by Kearney (data unpublished) in a cross between two families isolated from the King variety of Upland cotton and homozygous, respectively, for cream-colored and light yellow pollen (Figure 7).

In interspecies hybrids Balls, working with Upland × Egyptian, failed to get clear-cut segregation[4] but later reported F_1 as intermediate and F_2 as segregating in a 1:2:1 ratio[5] (p. 139, 140). McLendon[38] did not find monohybrid segregation in the hybrid Upland × Sea Island. Kearney[27], (pp. 26, 27) in Upland × Egyptian found yellow partially dominant with an F_2 distribution showing two modes, although the segregation was not sharply discontinuous. Corroborative evidence was obtained by this investigator in later studies of Upland-Egyptian hybrids (data unpublished). Harland[20] got similar results with his interspecies hybrids, there being 3:1 segregation if any shade of yellow is contrasted with "cream" but the action of modifying factors being shown by variation in the yellow class, the palest shade of yellow being scarcely distinguishable from cream (grade 0). Banerji[6] "in a natural cross of Sea Island cotton" of which the male parent presumably was not known, reports complete dominance of deep yellow over cream, 3:1 segre-

gation in F_2 and consistent results in his F_3 populations.

Harland[20] distinguished nine grades of pollen color in the numerous cottons of the American series which he intercrossed (Plate X, colored). His results were very similar to those he obtained in studying the inheritance of petal spot. His conclusions are summarized as follows (pp. 389, 390):

> A single genetic difference is involved in all crosses between any grade of yellow and grade 0. That is, yellow and pale cream form a simple pair of factors, which may be denoted as *P* and *p*. Modifying genes act on the basal gene for yellow, producing a complex series of shades from pale yellow 0.5 to deep golden 4.0. These modifying genes can be carried by grade 0 . . . *P* produces little effect when unsupported by modifiers, and the distinction between *P* and *p* is often hard to make in segregating families lacking such modifiers. . . . . In crosses between cottons of the same class, e.g., inter-Peruvian or inter-Upland, segregation is usually very sharp, owing to similar modifying factors being present in a homozygous condition in both parents. In the selfed back-cross (Upland × Sea Island) × Sea Island, an intensifier, *Q*, was demonstrated, having no visible effect except in presence of *P*. . . . . Grade 0 always breeds true in F_3 families or in selfed backcrosses.

Boll Apical Furrow

The exterior surface of the cotton boll is marked by shallow vertical furrows, extending from the apex to or nearly to the base of the boll and corresponding in number with the cells or locks, although the sutures in question are located midway between the internal partitions separating the cells. It is along these "midlock furrows" that the boll splits open when mature. The bolls of most varieties of Upland cotton have also very short furrows, extending from the apex, which overlie the internal partitions. These "apical furrows," as they may be termed, also occur less regularly in Sea Island cotton and in some varieties of Egyptian cotton.

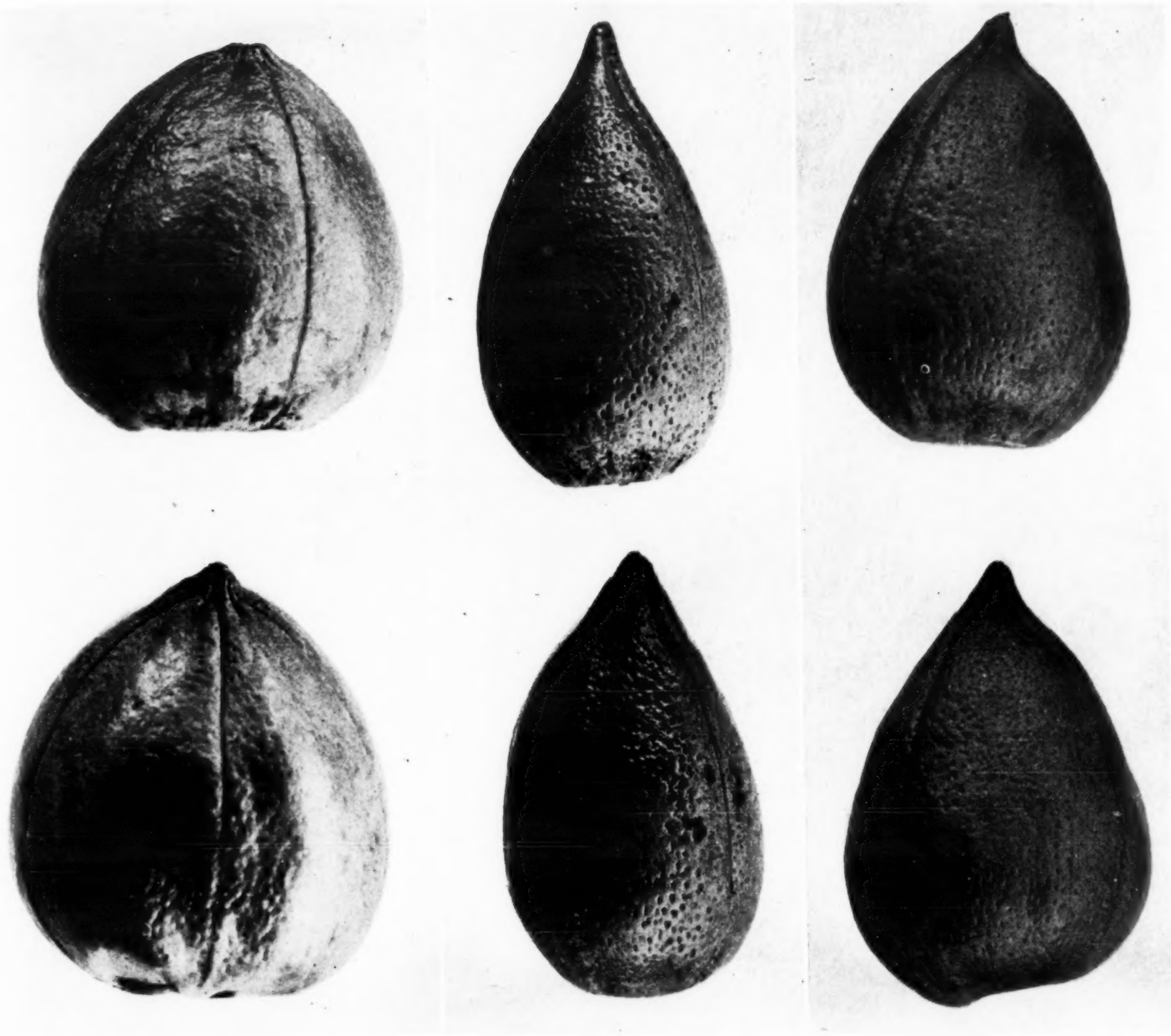
Kearney crossed the Holdon variety of Upland cotton, which has well-developed apical furrows (Figure 8), with Pima Egyptian cotton, which lacks these furrows and studied the inheritance of the character[27], (p. 27).* The furrows were absent in F_1 and the distribution in F_2, classifying as "furrow present" all plants which showed any trace of the character, suggested a dihybrid ratio of 9 (absent): 7 (present) (x^2 of departure 1.36). Absence, being dominant, was assumed to result from the combination of two dominant factors. Many of the F_2 plants had much longer and deeper furrows than the Upland parent.

Subsequent investigation (results hitherto unpublished) has given somewhat conflicting results. In Pima Egyptian × Holdon Upland F_2, grown in 1925, the ratio was 31 (absent): 24 (present), x^2 of the departure from a 9:7 ratio being practically 0. In Pima Egyptian × Acala Upland F_2, grown the same year, the ratio was 91 (absent): 93 (present), x^2 of the departure from a 9:7 ratio being in this case 3.45.

Of the Pima × Acala F_2 plants, 24 were represented by progenies grown in 1926, 13 of these F_2s having been classed as "furrow absent" and 11 as "furrow present." According to the assumption, of 13 furrow-less F_2s, 1.4 should be homozygous for absence of the furrow, 5.8 should give in F_3 a ratio of 9 (absent): 7 (present) and 5.8 should give in F_3 a ratio of 3 (absent): 1 present. Actually, there were 2 (possibly 3) F_3 progenies containing no plants with apical furrows, 4 progenies segregating in ratios approximating 9:7 and 6 segregating in ratios approximating 3:1. The observed classification of the 13 F_3 progenies therefore was 3 (?):4:6, while the expectation was 1.4:5.8:5.8, x^2 of the departure from expectation being 2.39.†

*The apical furrows were incorrectly designated "midlock furrows" in the publication cited.

† Taking as one array the 4 F_3 progenies which segregated in approximately 9:7 ratios,



BOLL FURROW IN SPECIES CROSS

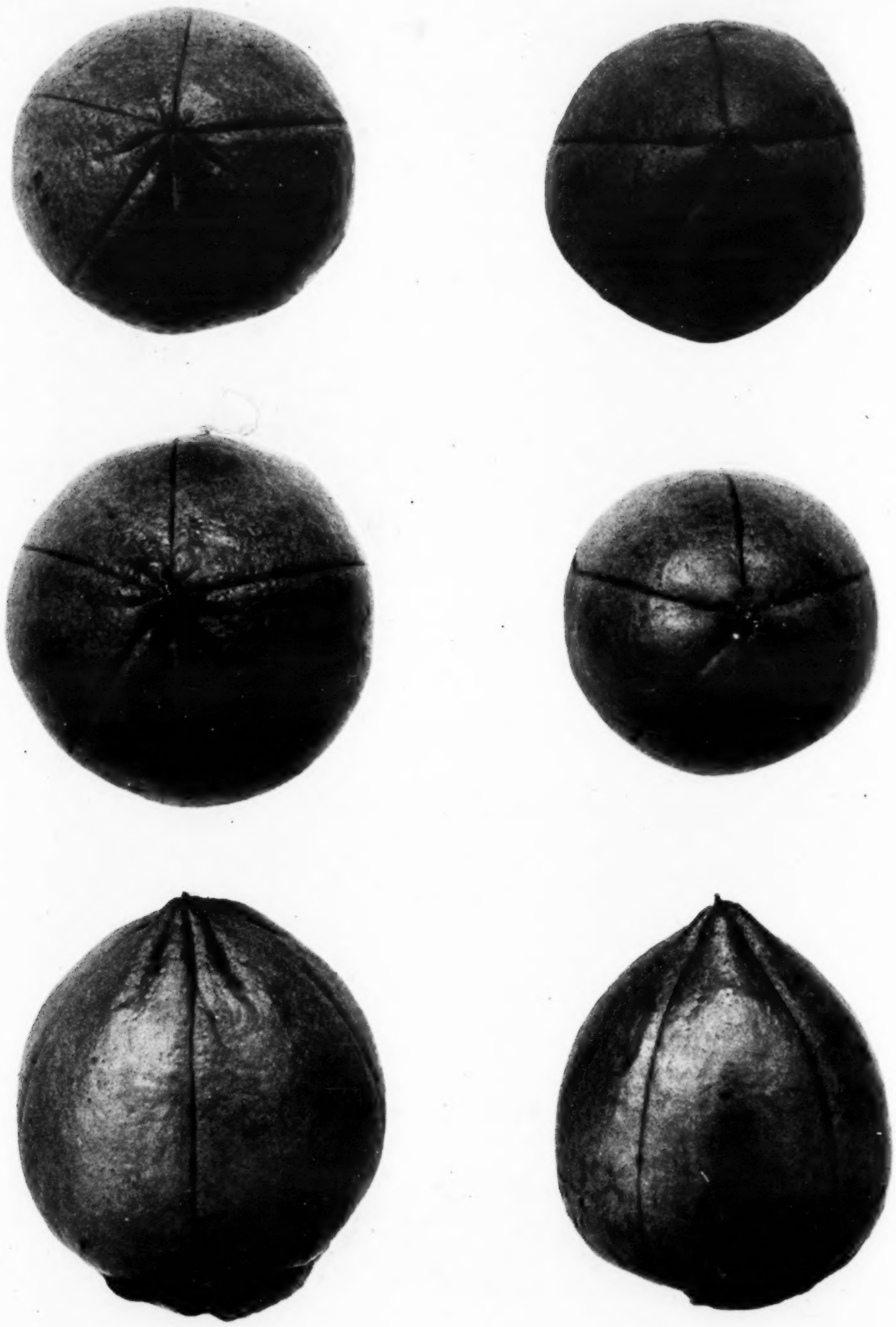
Figure 8

Inheritance of boll apical furrow in an interspecific hybrid *Gossypium hirsutum* x *G. barbadense*. A family of Upland cotton homozygous for presence of these short furrows (left) was crossed with a family of Egyptian cotton (center) homozygous for their absence. In F_1 (right) there were no apical furrows and in F_2 the segregation appeared to be dihybrid, 9 (furrows absent) : 7 (furrows present).

So far, the F_3 results from the later cross confirm, in fair measure, the initial assumption that absence of the furrow results from the combination of two dominant factors. But the behavior of the 11 F_3 progenies of Pima × Acala F_2 plants classed as "furrow present" was decidedly unfavorable to the theory. All such plants should have bred true for expression of the apical furrow, since presumably they lacked one or the other of the dominant factors supposed to condition absence. Actually, only 2 (possibly 3) of the 11 progenies contained no plants that were classed as "furrow absent."

Unpublished data obtained by Peebles and Kearney from hybrids between Pima Egyptian and the College variety of Upland cotton and between Pima and Sea Island, Pima having been the furrowless parent of both crosses, showed ratios in F_2 that were much

x^2 of the departure from expectation in this population (63 plants) was 0.38. Taking as one array the 6 F_3 progenies which segregated in approximately 3:1 ratios, x^2 of the departure from expectation in this population (89 plants) was 0.09.



PRESENCE AND ABSENCE OF APICAL FURROWS

Figure 9

Bolls of a family of the Lone Star variety of Upland cotton, homozygous for presence of conspicuous apical furrows (left); and bolls of a family of the College variety of Upland cotton, homozygous for absence of the apical furrows (right). Inheritance of this character, in a cross between these families which belong to the same species (*Gossypium hirsutum*) is being investigated at the U. S. Field Station, Sacaton, Arizona. Natural size. Photograph by H. F. Loomis.

closer to 3:1 than to 9:7.

This character, like petal spot, is extremely variable. An individual plant may produce as many as 20 bolls showing no trace of an apical furrow and then produce a boll showing a faint trace at the apex. Whether to place such a plant in the "furrow present" class along with plants on which every boll has deep apical furrows extending nearly the entire length of the boll, is one of the problems encountered in studying the inheritance of this character in interspecies crosses. In all probability the parental species differ in several modifying factors as well as in whatever main factors may be involved.

As is the case with so many other characters, solution of the problem must await the study of crosses between more closely related forms. Such material is now available, two families of Upland cotton having been isolated at Sacaton, Arizona, which are homozygous, respectively, for presence and absence of apical furrows (Figure 9).

Boll Color

Crossing an Upland cotton, in which the unripe boll is light green, with Sea Island cotton, in which the boll color is deep green, Kulkarni and Khadilker[34] reported intermediacy in F_1 and a 1:2:1 ratio in F_2. It seems improbable, however, in view of the known behavior of other color characters in interspecies hybrids, that the situation was as simple as is indicated by the data given by these investigators.

Boll Pubescence

Peebles[40] reports the occurrence, in F_2 of an Egyptian-Upland hybrid, of a plant having numerous hairs on the surface of the boll, even when full-grown. Neither parental family showed this character although, in the Egyptian family, a few hairs are present on the ovary but disappear after fertilization. The character bred true so far as the small size of the F_3 progeny (6 individuals) permits a conclusion. It was conjectured that the expression of this character may depend upon the combination of two recessive factors, one of which probably was derived from each of the parents of the original cross, but the data now available are far too scanty to support a definite conclusion.

Seed Fuzz, Quantity and Distribution

The seeds of most of the cultivated species and varieties of Gossypium are more or less covered with short hairs or fuzz in addition to the long lint hairs. The two kinds of hairs differ in dimensions and sometimes in color, but both are simple outgrowths of the outer epidermal cells of the seed coat. In various types of cotton, plants occur in which the seed coat is entirely devoid of fuzz, the seeds being perfectly naked when the lint is removed. Such plants are of rather frequent occurrence in Upland cotton, the absence of fuzz being usually correlated with very sparse lint. There occurs also the condition denominated "smooth" by Kearney and Harrison[31], "fuzzy tip" by Carver[8] in which the fuzz is greatly reduced in quantity and is localized at the hilum end of the seed, often also with a trace at the other end and along the raphe. "Smooth" or "fuzzy tip" seeds are especially common in the South American Tree or Peruvian group, being, in fact, characteristic of several of the cultivated Sea Island and Egyptian varieties. In Upland cottons this form appears to be rarer than naked (entirely fuzzless) seed.

The results obtained in crossing naked-seeded with entirely fuzzy-seeded forms of the same species will be considered first. Thadani[45,46] crossed members of a naked-seeded Upland family which he designated "No Lint" with representatives of each of five Upland varieties having entirely fuzzy seeds. He reported complete dominance of naked seed in F_1 and 3:1 segregation in F_2. Similar results

in crosses between Upland cottons were obtained by Kearney and Harrison[31] Carver[8] and Griffee and Ligon[10]. In the cross made by Kearney and Harrison[31], (combination 3, pp. 202, 203, Fig. 4) x^2 of the departure from a 3:1 ratio in F_2 was 0.6, when plants having naked or nearly maked seeds were contrasted with plants having entirely fuzzy seeds, but 4 of the 22 dominants were recorded as having the seeds "fuzzy-tipped" rather than completely naked.* Carver[8] concluded from the results of intercrosses among 5 naked-seed Upland families of independent origin that all had the same gene for naked (N). Fyson[9] reported dominance of naked-seed and monohybrid segregation in crosses between a naked-seeded and a fuzzy-seeded Indian cotton.

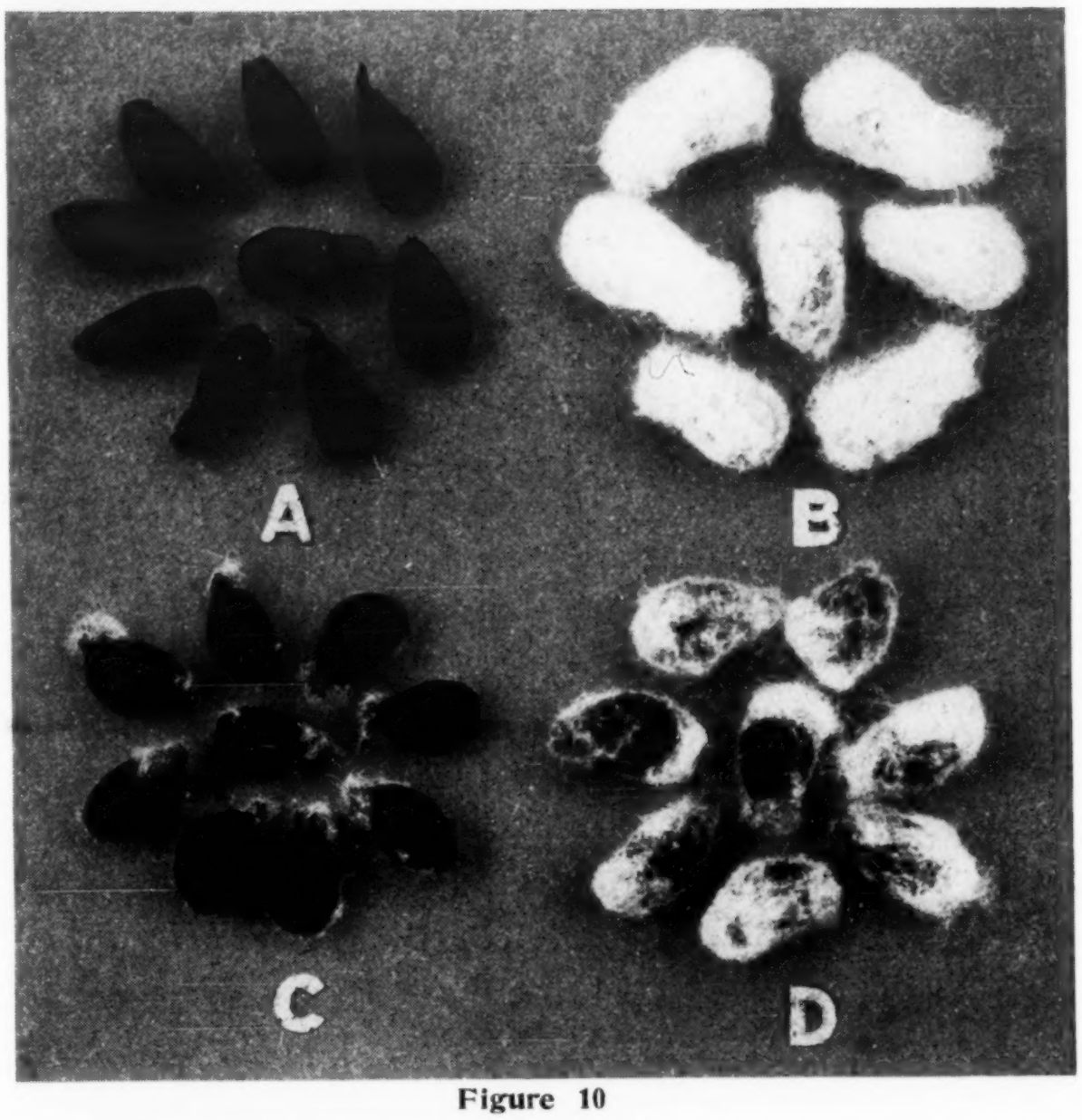


Figure 10

Seeds with lint removed, showing the range of fuzziness in Upland and Egyptian cottons. A naked-seeded Upland, B, entirely fuzzy-seeded Upland, *C*, smooth-seeded Egyptian, *D*, fuzzy-seeded Egyptian. These forms constitute an allelomorphic series, with dominance of A to B, C and D, dominance of B to C and D and dominance of C to D. (Photograph by R. L. Taylor).

Crosses within the same species where the contrast is between a more fuzzy and a less fuzzy condition rather than between presence or absence of fuzz have given diverse results. Balls[5], (p. 143) who studied crosses between Egyptian cottons, found that "in all cases they have given a simple 3:1 ratio, more fuzz being dominant over less fuzz, and expectation has been fulfilled in F_3." On the other hand, Thadani[46], found dominance of the less fuzzy conditions in crosses between Upland cottons.

Kearney and Harrison[31], (pp. 194-197) crossing a "smooth-seeded" (fuzzy tip) form of Pima Egyptian cotton with a form of the same variety having the seeds almost covered with fuzz, found the "smooth" condition completely dominant in F_1 and close approaches to 3:1 ratios in F_2†. All fuzzy-seeded F_2s bred true. Of 20 smooth-seeded F_2s tested by growing F_3 progenies, the published data indicated that only 2 were homozygous but later evidence (unpublished) indicates that 4 should have been thus classified. Since the number of homozygotes should have been $20/3 = 6.66$ instead of 4, x^2 of the departure from the expected ratio of 2 (heterozygous) : 1 (homozygous) progenies is 1.60.‡ The evidence, therefore, is satisfactory

* It is probable that closer inspection would have shown a larger number of plants whose seeds were not perfectly naked, since the unpublished results of later investigations point to the conclusion that the heterozygous F_2s of such a cross may be recognized by the presence on the seed of minute quantities of fuzz or of the persistent bases of lint hairs.

† Only 4 of the 17 F_2 progenies gave a x^2 for the departure from a 3:1 ratio greater than 0.7. For the combined F_7 population (381 individuals) x^2 of the departure was 1.33.

‡ For the 16 segregating F_3 progenies as one array (298 individuals) x^2 of the departure of the observed proportions of smooth and fuzzy from the 3:1 ratio is 0.76.

that almost entirely fuzzy is a simple recessive to smooth (fuzzy-tip) within the Pima variety of Egyptian cotton.

Crosses of Upland cottons made by Carver[8] between fuzzy tip and entirely fuzzy-seeded families, showed dominance of fuzzy tip (*Ft*) but the segregation was not clear-cut. It was concluded that "the tip brush of fuzz is fundamental; and that the presence of fuzz over the seed is controlled by modifying factors." Crossing a naked-seed family (*N ft*) with a fuzzy tip family (*n Ft*) he obtained in F_2 a ratio approaching the 12:3:1 expected if entirely fuzzy is the double recessive, only 16 of the 321 F_2 plants having been entirely fuzzy-seeded.*

The inheritance of seed fuzziness, as of other characters, is more complex in inter-species hybrids. Consistent results (with a single exception) were obtained with Upland × Egyptian by Balls,[3, 4] Kearney,[27] Thadani[46] and Kearney and Harrison[31]; and with Upland × Sea Island by McLendon[38] and Kulkarni and Khadilker[34]. In all of these crosses the Egyptian or Sea Island parent represented a partly fuzzy condition and the Upland parent an entirely fuzzy condition. The more fuzzy condition was dominant† and there was an absence of clear-cut segregation in F_2, although Balls[5] (p. 143) reports that "naked seed breeds true." This implies that there were segregates from his Upland-Egyptian hybrids, with seeds entirely devoid of fuzz, an unusual occurrence. In the Upland × Egyptian studied by Kearney[27] (Fig. 41, p. 26) the F_2 distribution was continuous and only 5 of the 193 plants equalled the Egyptian parent in the scantiness of fuzz on their seeds, none having been naked-seeded. Some of the segregates had much longer fuzz hairs than the fuzzier seeded (Upland) parent, indicating that the parental species have different modifiers for this character.

In a cross between an Egyptian form having partly fuzzy seeds and naked-seeded Hindi, a near relative of Upland cottons, Balls[5] (p. 144) found dominance of entire fuzz and, in F_2, 123 plants entirely fuzzy, 7 partly fuzzy and none naked-seeded. He states that a backcross of Hindi × Egyptian on Hindi "yielded simple segregation of the naked Hindi seed in F_2."

Fyson[9] reports that in the hybrid *G. peruvianum* (naked-seed form) × *G. hirsutum* (Upland with entirely fuzzy seeds) the naked condition was dominant. Kearney and Harrison[31] (combinations 7 and 8, pp. 206-209) crossed a naked-seed Upland on two families of Pima Egyptian, one of which had almost naked (fuzzy tip) seeds while the other had the seeds about half-covered with fuzz. In both cases naked-seed was dominant. These results, considered with Fyson's, suggest that presence of fuzz in any degree is recessive to its complete absence in inter-species as well as in intra-species crosses, but dominance of fuzzy seed to naked seed in the inter-species cross (Egyptian × Hindi) mentioned by Balls and dominance of "tufted" seed in Peruvian cotton to naked seed in an intraspecies cross (Peruvian × Peruvian) mentioned by Harland[22] make it unsafe to generalize in the present state of our knowledge.

In inter-species hybrids between Pima Egyptian families having from one-half to three-fourths of the seed surface covered with fuzz and Upland families having entirely fuzzy seeds,

---

* x^2 of the departure from 1:15 (as computed by T. H. Kearney) is 0.84.

† The exceptional case is reported by Thadani who states that, while in most of his Egyptian-Upland crosses the more fuzzy condition was dominant, in the cross Yuma Egyptian × Red Leaf Upland, in which the Egyptian parent was "fuzzy tip" and the Upland parent entirely fuzzy, the less fuzzy condition was dominant. Since Kearney's unpublished data on a cross between Yuma and Lone Star Upland show dominance of the entirely fuzzy (Upland) condition, it would appear that Red Leaf may have a different factor for fuzziness than most varieties of Upland.

Kearney and Harrison[31] (combinations 4, 5 and 6, pp. 203-205, figs. 5 and 6) found the Upland degree of fuzziness dominant in F_1 and a range in F_2 from somewhat greater fuzziness than was shown by the Egyptian parent to beyond that of the Upland parent. The fact that the two species represented by Upland and Egyptian cotton, respectively, have different genes for this character is clear from comparison of the results from two of the crosses made by Kearney and Harrison[31] (pp. 209, 210). These are the intra-species cross naked seed Upland × entirely fuzzy Upland (combination 3) and the inter-species cross smooth-seed (fuzzy tip) Egyptian × entirely fuzzy Upland (combination 9). Since the same homozygous family furnished the entirely fuzzy Upland parent of both crosses, and since F_1 was uniformly naked-seeded in the first cross and uniformly entirely fuzzy-seeded in the second, it follows that the factors for nakedness in Upland and smoothness (fuzzy tip) in Pima Egyptian are not the same, the former being dominant and the latter recessive to Upland fuzziness.

The results obtained by Kearney and Harrison, concordant in the main with those of other investigators, indicate the existence of four allelomorphs (Figure 10), which may be designated:

A (naked seed in Upland cottons).

B (fuzzy seed in Upland cottons).

C (smooth seed or fuzzy tip in Pima Egyptian).

D (fuzzy seed in Pima Egyptian).

It appears that *A* is dominant to *B*, *C* and *D*; *B* to *C* and *D*; and *C* to *D*. It also seems probable that different modifying factors exist in the two species. The relation of *C* to *Ft*, Carver's gene for "fuzzy tip" in Upland cottons, should be investigated.

A somewhat different series of allelomorphs is listed by Harland[22] (pp. 312, 313) who has not, however, published his experimental data:

> Five factors have been identified governing the distribution of fuzz on the seed coat. These factors produce various types of fuzzy, tufted and naked seeds, respectively.
>
> *T*. The factor *T* produces a tuft on the apex of the seed which behaves as a simple dominant to naked. Found only in the Peruvian group.
>
> *A*. A dominant tufted factor found in Meade [Upland] dominant to the tufted of Sea Island, and to the fuzzy of *tomentosum*.
>
> *Z*. A dominant fuzz factor found in most Uplands, dominant to Sea Island tufted, present also in *tomentosum*.
>
> *F*. A fuzz factor dominant over Meade tufted.
>
> *N*. A factor for naked seed found in Upland, completely dominant over all other forms of fuzz distribution.
>
> In addition to these five factors, there are minor modifying factors concerned in producing gradations in the fuzzy and tufted groups.

Harland's factors *N* and *Z* presumably are identical with the factors *A* and *B* revealed by the investigation of Kearney and Harrison, but factors *T* and *A* of Harland seem to be different from any factors previously discovered.

The difficulty of classifying populations resulting from crosses between families differing in the quantity and distribution of fuzz on the seeds, and particularly the identification of modifying genes which doubtless exist, is enhanced by the great amount of fluctuating variation to which this character, like petal spot, is subject. Quantitative evidence on this point is given by Kearney and Harrison.[32]

This character offers the only example so far detected among allelomorphic characters in cotton of dominance of the aberrant, presumably mutant, condition, naked seed being dominant to fuzzy seed in Upland cottons. Since fuzziness is closely associated with abundant lint, it might be conjectured that nakedness of the seed coat is the primitive condition in *Gossypium hirsutum* and that selection during countless generations for more abundant lint has brought with it increasing fuzziness. An objection to generalization of this view is that the seeds of most of the truly wild species of Gossypium (Kearney[30]) are covered with short hairs (fuzz) but lack the long lint hairs. *(To be Concluded)*